ABSTRACT

Title of Document:	Local versus regional processes impacting insect diversity loss from urban headwater streams
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Watershed urbanization alters hydrologic, geomorphic, and chemical properties of stream ecosystems and decreases water and habitat quality for stream fauna. The resulting loss of insect diversity from urban streams and the mechanisms resulting from in-stream habitat degradation are well documented. In this study, I focus on how urbanized terrestrial landscapes contribute to diversity loss from stream insect communities. Characteristics of fragmented urban landscapes likely increase mortality, reduce reproduction, and block dispersal by adult stream insects, which can contribute to reduced diversity. I compared the adult caddisfly assemblage among 4 urban and 4 rural headwater streams and found no difference in abundance but lower taxa richness at urban than rural headwaters. Poor in-stream and terrestrial environmental conditions likely caused decreased adult diversity at urban headwaters. I expanded this study by comparing adult and larval assemblages residing in the same 8 headwater streams.

Patterns of larval and adult taxa richness, assemblage composition, and urban landscape structure at individual streams suggested that constrained dispersal through urban landscapes (a regional process) and poor environmental conditions in the stream (a local process) both contributed to larval diversity loss from urban headwaters. I also compared flight morphological characteristics of 2 caddisfly species restricted to rural headwaters to 4 species that commonly immigrated to urban headwaters. Wing length and wing aspect ratio did not differ between these 2 groups, but species specific differences for both measures indicated that flight ability may have supported immigration to urban headwaters for certain species. Finally, I used multimodel inference testing to determine what combination of geographic distance, environmental dissimilarity, and land use between streams best explained patterns of taxonomic dissimilarity between in-stream insect communities within 4 Maryland watersheds. All three variables together, based on Euclidean geographic distance, provided the best model fit and supported the hypothesis that regional and local processes structure stream insect communities simultaneously. The overall conclusion from my work was that site specific characteristics of terrestrial urban landscapes caused species specific constraints on adult insect migration that contributed to larval diversity loss from urban streams simultaneously with poor in-stream habitat and water quality.

LOCAL VERSUS REGIONAL PROCESSES IMPACTING INSECT DIVERSITY LOSS FROM URBAN HEADWATER STREAMS

By

Robert Francis Smith

Dissertation submitted to the Faculty of the Graduate School of the
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Foreword

With the recommendation of the dissertation director (William O. Lamp), and with the endorsement of the Entomology program Graduate Director (Paula M. Shrewsbury), chapter 1 of this dissertation is included as a previously published work. The citation for this publication is as follows:

Smith, R.F., L.C. Alexander and W.O. Lamp. 2009. Dispersal by terrestrial stages of stream insects in urban watersheds: a synthesis of current knowledge. Journal of the North American Benthological Society 28:1022-1037.

As directed in the graduate catalog for chapters previously published as coauthored works, I state that I was responsible for the inception of the manuscript and the majority of the manuscript preparation. This work was reformatted to meet the requirements for dissertations, but all other aspects of the published manuscript, including the use of first person plural, were used in this document. A letter was sent to the Dean of the Graduate School certifying that inclusion of this previously published work in this dissertation has the approval of the dissertation committee, the dissertation advisor, and the Graduate Director. A copy of this letter is included in Appendix A.

Dedication

I dedicate this work to my friends and family that wished me luck at the beginning, supported me along the way, but are not here to see what their love and support allowed me to accomplish. I also dedicate this work to my parents, who have provided unwavering support of all my academic endeavours. I also dedicate this work to my daughter Elizabeth Guider Smith for whom I hope this research may play some part in conserving the natural beauty of a healthy stream ecosystem for her to enjoy with her children someday. Finally, and most importantly, I dedicate this work to my wife who has selflessly supported me during my graduate career. I couldn't have asked for a better partner in life and mother to my daughter. Every success I've had is because of her love and support. ILYMTTSATMATSITS

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In addition to those mentioned above, my coauthors and I specifically acknowledge for chapter 1, Bridget Wille-DeLay, Alan Leslie, Susan Lombardi, and Lauren Culler for reviewing earlier versions of the manuscript used as the basis for this chapter. We thank Margaret Palmer, with whom we have had many discussions about the importance of understanding the natural history of adult aquatic insects in urban watersheds. We also thank 2 anonymous referees and Alison Purcell for providing comments that greatly improved the manuscript used as the basis for this chapter. Last, we thank Allison Roy, Seth Wenger, and Alison Purcell for organizing the Second Symposium on Urbanization and Stream Ecology and providing us the opportunity to present the manuscript used as the basis for this chapter. Preparation of the manuscript used as the basis for this chapter was supported by a grant from the US Department of Agriculture Biotechnology Risk Assessment Grant, number 2005-33522-16456.

In addition to those mentioned above, I specifically acknowledge for chapter 2, Erik Pilgrim from the US EPA for performing the DNA barcoding work. This manuscript, when published, will be submitted as a co-authored, collaborative work. DNA barcoding work was done free of charge by the US EPA, and this data improved this chapter greatly. I also thank Ken Staver of the Wye Research and Education Center for performing the water chemistry work free of charge.

In addition to those mentioned above, I specifically acknowledge for chapter 5, Matt Baker who provided invaluable instruction on the use of GIS for performing research on stream ecology. Dr. Baker also provided guidance during the development of

this work. I also thank Dilip Venugopal for providing guidance on programming GIS, performing the statistical analysis, and reviewing this chapter. When completed, this chapter will be published as a collaborative work with Matt and Dilip. I also thank the MD-DNR for providing the Maryland Biological Stream Survey data used in chapter 5. I also thank the University of Maryland - Department of Entomology for purchasing a software license for Arc Desktop and for purchasing a desktop computer specially designed for performing GIS analysis. Finally, I thank Greg Hess for providing much needed technical, software, and hardware support for the GIS analysis used for this research.

In addition to everyone above, I especially want to acknowledge my advisor Dr. Bill Lamp for his guidance during my graduate career and support of this research. Bill provided financial and logistical support for all facets of my dissertation research. More than anything, however, I thank Bill for the unconditional support and patience he showed as I learned to be a stream ecologist. Even up until the day of submission, he provided careful and thorough guidance without judgement. He has a keen ability to see the potential in people and an even greater ability to help them reach that potential. While many doubted my abilities to perform this (or any) research, Bill saw something in me when I entered his lab that even I wasn't sure was there. My development as a scientist and my ability to complete the research presented in this dissertation are due directly to his abilities as an educator and scientist, and I only succeeded because he was my advisor.

Table of Contents

List of Tables

List of Figures

Chapter 1: Dispersal by terrestrial stages of stream insects in urban watersheds: A synthesis of current knowledge

Abstract

Adult dispersal and completion of life cycles by aquatic insects are essential for the persistence of populations, colonization of new habitats, and maintenance of genetic diversity. However, life-cycle stages and processes associated with the terrestrial environment often are overlooked when the effect of watershed urbanization on the persistence of insects associated with streams is examined. We reviewed and synthesized current literature on the known effects of watershed urbanization on the terrestrial stage of stream insects. Some research has directly examined the effects of watershed urbanization on dispersal, but much of the evidence we present is indirect and from related studies on aquatic insect life-history traits and dispersal abilities in nonurban watersheds. Our goal is to provide examples of potential impacts that warrant further study, rather than to provide a comprehensive review of all life-history studies. We discuss how watershed land use, riparian condition, and habitat quality affect: 1) adult fitness, 2) adult dispersal, and 3) habitat fragmentation, and 4) how these factors interact with species traits. In general, we found that the local- and landscape-scale changes to stream, riparian, and upland habitats that typically result from anthropogenic activities have the potential to prevent the completion of aquatic insect life cycles and to limit adult dispersal, and therefore, can affect population persistence. When considered within the spatial context of dendritic stream networks, these effects, particularly those on adult dispersal, might have important implications for design and assessment of restoration projects. We discuss a framework for how to determine the relative importance of effects on specific life-cycle stages and processes for the absence of larval populations from urban streams. Overall, more research on terrestrial life-cycle stages and processes and on adult dispersal is required to understand how urbanization might affect population persistence of insects in urban streams.

Introduction

Anthropogenic alterations to natural landscapes can lead to loss of native populations (Pickett et al. 2001, McKinney 2002). The change from natural to urban land use in watersheds generally degrades habitat and water quality for stream-dwelling insects (Sweeney 1993, Paul and Meyer 2001, Walsh et al. 2001, 2005, Roy et al. 2003). These effects can cause species loss, increased dominance of taxa tolerant of poor habitat, and decreased diversity at the community level (Allan and Flecker 1993, Paul and Meyer 2001, McKinney 2002, Walsh et al. 2005).

Degradation of the aquatic environment in urban streams has been linked to patterns of decreased diversity (Allan and Flecker 1993, Allan 2004, Moore and Palmer 2005, Urban et al. 2006), but direct effects on the aquatic stage of stream insects do not represent all potential mechanisms involved in loss of insect taxa. All stages of the insect life cycle must be completed for a population to sustain itself, or the population must be rescued by immigrants from neighboring populations. However, research to date has focused on the effects of watershed urbanization on aquatic insect development, survival, and movement within the stream (e.g., Petersen et al. 2004), which excludes one or more life stages of many aquatic insects. The anthropogenic alteration of natural landscapes can affect both instream and terrestrial stages of aquatic insects. Terrestrial habitats of adult aquatic insects include stream banks, riparian areas, and upland areas, and aquatic insects interact with biotic and abiotic components of these habitats. Anthropogenic activities in a watershed can alter upland and riparian habitat structure and, thus, affect adult aquatic insect fitness and dispersal (McIntyre 2000).

Understanding the effects of watershed urbanization on the entire life cycle of stream insects is important for conserving and restoring populations and communities in urban watersheds. Aquatic insects are important components of stream ecosystem function (Wallace and Webster 1996, Covich et al. 1999) and are important food resources for higher trophic levels in aquatic (Huryn and Wallace 2000) and terrestrial habitats (Gray 1993, Sabo and Power 2002, Kato et al. 2003, Briers et al. 2005, Fukui et al. 2006). Impacts to terrestrial adult stages might indirectly affect ecosystem function because adults play a vital role in population persistence. Stream insects also are used as bioindicators of stream health (e.g., Rosenberg and Resh 1993, Barbour et al. 1999, Karr 1999, Bonada et al. 2006), and a full understanding of how watershed urbanization affects population persistence has important implications for their utility for assessing stream health or restoration success.

The critical role of terrestrial life stages in regional adult dispersal makes understanding the effect of urbanization on the entire life cycle of stream insects particularly important (Petersen et al. 2004). Dispersal, defined by Bilton et al. (2001, p.160) as the ‘‘movement of individuals or propagules between spatially (or temporally) discrete localities or populations,’’ can directly affect population dynamics (Palmer et al.

1996, Fagan 2002, Grant et al. 2007), as well as population genetic structure and local adaptation (Wright 1938). Drift by larval insects has been well studied (Waters 1972, Allan 1995, Huryn et al. 2008), and long distance movements between watersheds by drifting and crawling is unlikely (Jackson et al. 1999, but see Elliot 2003). Research on adult dispersal traditionally has focused on measuring distance, direction, and flight behavior in various terrestrial habitats (Bilton et al. 2001), and only a few studies have attempted to determine how terrestrial environments affect transport between 2 adjacent habitats (e.g., Macneale et al. 2005, Blakely et al. 2006). Even in species with very short adult stages, restricting terrestrial dispersal can constrict population growth or lead to population loss, independent of impacts to aquatic stages from instream habitat degradation (Power et al. 1988, Enders and Wagner 1996). On the other hand, dispersal can mitigate some negative effects of watershed urbanization by enabling recolonization of streams if habitat and water quality improve (Palmer et al. 1997, Bond and Lake 2003, Lake et al. 2007). Ultimately, the loss or maintenance of populations related to insect dispersal ability will affect regional patterns of species biodiversity in streams (Vinson and Hawkins 1998).

We discuss the diversity of aquatic insect life cycles, with a focus on use of terrestrial environments by aquatic insects. We explored what is currently known about the effects of watershed urbanization on: 1) adult fitness, 2) adult dispersal, 3) habitat fragmentation, and 4) the interaction of these factors with species traits. We focused on direct effects to terrestrial stages of aquatic insects and did not cover impacts to larval stages that can influence dispersal ability (e.g., Stevens et al. 1999, Plaistow and Siva-Jothy 1999). We found that few studies have provided direct empirical evidence of urban landuse effects on the terrestrial stage of aquatic insects. As a result, we included relevant studies on dispersal and life-history traits of aquatic insect species in nonurban terrestrial habitats. We stopped short of providing a review of all instances of life-history traits and adult behaviors that could relate to potential impacts to adult insects in a typical urban watershed. Instead, we have provided examples of these potential impacts and suggested areas that require further study. We also discuss the role of the terrestrial environment for stream restoration and species conservation and a potential framework for identifying the effects of urbanization on developmental stages and life-cycle processes of stream-dwelling insects.

Aquatic Insect Life Histories and Dispersal

Life cycles and species traits

Aquatic insects have complex life cycles with distinct developmental stages that differ in their requirements to use aquatic and terrestrial habitats (Wilbur 1980, Werner and Gilliam 1984, Huryn et al. 2008). Figure 1.1 illustrates a generalized life cycle of an aquatic insect species and includes the life stages and life-cycle processes that, if affected by urbanization, could lead to population loss. In our review, we refer to aquatic insects as being in the aquatic stage or the terrestrial stage. Aquatic insects generally have an immature stage confined to living, feeding, and dispersing (e.g., drift or crawling) in the aquatic environment. Adult stages for most aquatic insect taxa are terrestrial, but some species in the orders Coleoptera and Hemiptera are exceptions (Polhemus 2008, White and Roughly 2008). Instream dispersal is possible by crawling, swimming, and drift during the aquatic stage. Dispersal during the terrestrial stage occurs by flight, crawling over land, and surface skating over the water. Aquatic coleopteran and hemipteran adults

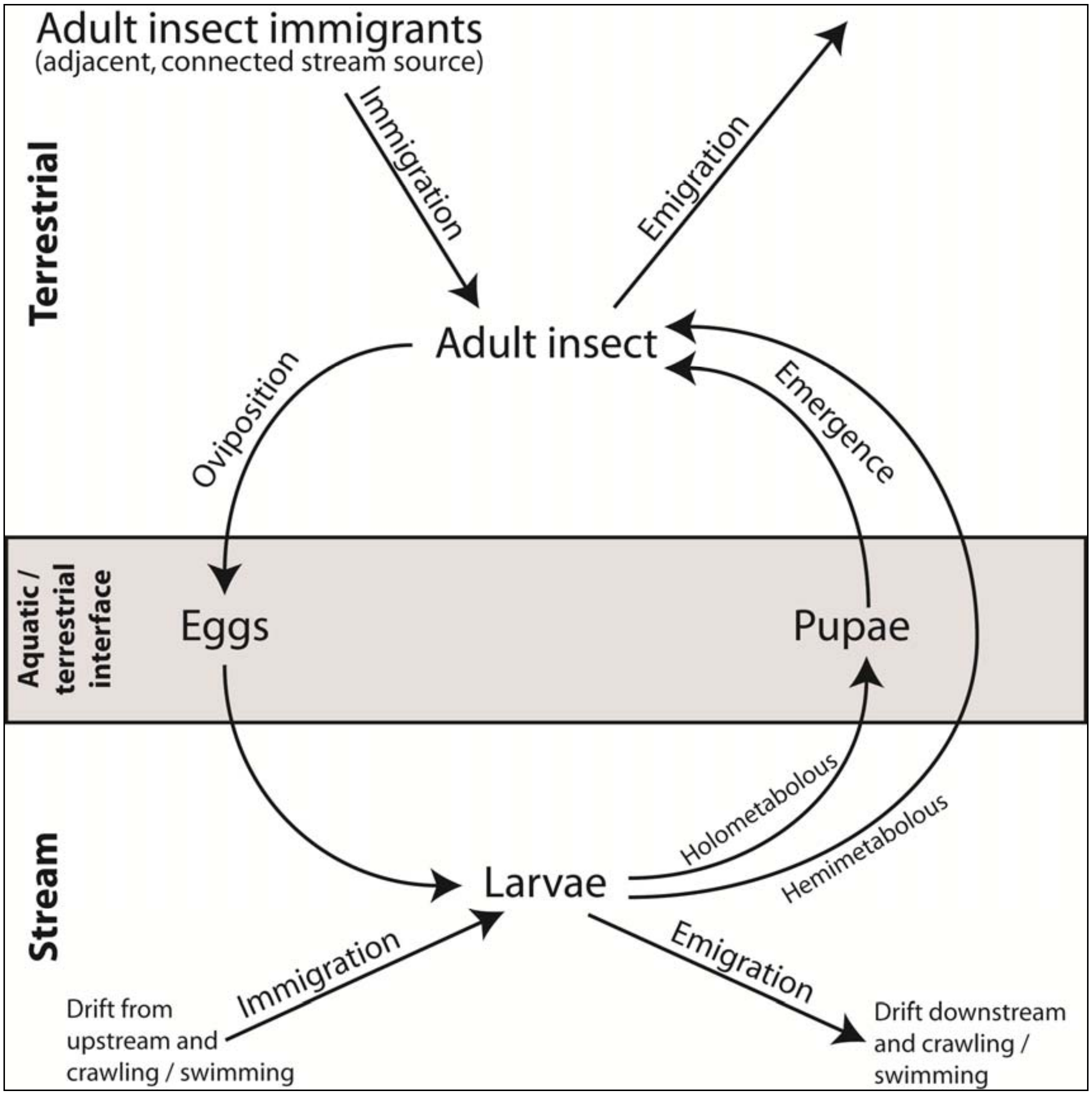


Fig. 1.1. Diagram of a generalized aquatic insect life cycle for holometabolous and hemimetabolous insects. The complete life cycle includes aquatic and terrestrial stages. The association of pupal and egg stages with the terrestrial and aquatic environments differs among species and often involves both stages. As a result, we describe these stages as being part of the aquatic/terrestrial interface. Any breakdown in the life cycle, increase in emigration, or barrier to immigration can contribute to population loss.

usually have the ability to leave the aquatic environment, disperse through the terrestrial environment, and colonize another aquatic habitat (Polhemus 2008, White and Roughly 2008). Thus, the adults of some taxa are aquatic-stage and terrestrial-stage dispersers simultaneously. Adults of other taxa of aquatic insects cannot return to an aquatic environment except to oviposit. The interactions of egg and pupal stages with the terrestrial and aquatic environments differ among species, but generally these stages are associated with the interface between aquatic and terrestrial environments (Huryn et al. 2008). In addition, adult oviposition behavior and emergence of larvae and pupae occur within or in proximity to the aquatic environment and represent processes responsible for bridging the aquatic–terrestrial interface during aquatic insect life cycles (Huryn et al. 2008).

The diversity of life cycles and dispersal habits limits our ability to generalize the effects of urbanization on terrestrial stages across all aquatic insects. Use of the terrestrial environment by adults and transport of adults among habitats differ among orders, among species within orders, and between adult and larval stages of the same species (Huryn et al. 2008). For example, some stream insects feed extensively as adults (e.g., Odonata; Corbet 1999), whereas others do not feed at all (e.g., Ephemeroptera; Brittain 1982). All orders of aquatic insects possess some taxa that are capable of flying. However, flight capability can differ widely among species within an order and among individuals within a species (e.g., Plecoptera; Hynes 1976), or might change during the lifetime of an individual (e.g., wing histolysis in reproductive stages of species of Gerridae; Kaitala and Huldén 1990). Some generalizations can be made at the order level, but exceptions are common and life-history strategies vary greatly at the species level.

From an instream perspective, aquatic stages respond to urbanization with increased mortality, decreased production, or increased drift out of the stream reach, which cause loss of the larval population from the stream regardless of impacts to terrestrial stages (reviewed by Paul and Meyer 2001). In contrast, terrestrial conditions and the aquatic–terrestrial interface might cause similar declines in population size by preventing successful adult emergence, mating, or oviposition, or by limiting adult survival. Expansion of our focus to include the entire insect life cycle suggests additional avenues by which watershed urbanization can lead to population loss, with or without affecting aquatic stages.

Function and extent of adult dispersal

Movement by aquatic insects at the regional scale is important for colonization of new habitats, escaping unsuitable habitats, and recruitment of neighboring populations. Recruitment occurs through immigration of adult or larval individuals or through addition of offspring from viable eggs to an uninhabited area or an existing population. Individual insects can be added to a population through movement of the aquatic stages, but most recruitment for successive generations of aquatic insect populations occurs by addition of eggs from adult female oviposition (Bunn and Hughes 1997). Most species of aquatic insects reproduce sexually, although parthenogenesis occurs in most aquatic insect orders (Chapman 1998) and is common in mayflies (Sweeney and Vannote 1987, Funk et al. 2006).

Dispersal also can be important for supplying recruits to upstream reaches that lose individuals through downstream drift. Adult aquatic insect flight often is oriented in an upstream direction (Pearson and Kramer 1972, Neves 1979, Coutant 1982, Winterbourn and Crowe 2001, Macneale et al. 2005) and might have evolved in response to the loss of immature individuals that drift downstream (Müller 1982). Hershey et al. (1993) found that the observed preference of a mayfly species to fly upstream and oviposit compensated for the loss of individuals drifting from upstream reaches. Anholt (1995) found that persistence of populations in upstream reaches also could be explained by density dependence of birth and death rates upstream, but concluded that population persistence still required occasional movement of adult individuals upstream.

Dispersal that increases individual fitness acts as a selective force affecting persistence and spatial distribution of populations connected by gene flow (Gandon and Michalakis 2001). Gene flow, the transfer of alleles from one population to another, occurs when colonization or recruitment is followed by multiple generations of successful outbreeding (Bilton et al. 2001). Flow of novel alleles into a population is an important source of genetic variation, but even without new variants, gene flow maintains genetic diversity locally by increasing the effective size of the population and slowing the rate at which shared alleles are lost at random through genetic drift (Wright 1938). Limited gene flow can facilitate local adaptation, but small, isolated populations lose genetic variation through genetic drift and, over time, can become subject to the detrimental effects of inbreeding (Frankel and Soulé 1981). Urban environments couple human and aquatic insect populations in ways that produce selection pressures with complex effects on the fitness of members in both groups. In Cali, Columbia, insecticide applications to control the Dengue virus vector *Aedes aegypti* produced locally intense selection pressures that interacted with high levels of gene flow and resulted in rapid changes to mosquito population genetic structure, vector competence, and resistance to insecticides that varied independently among the sites and times evaluated (Ocampo and Wesson 2004). The prevalence of multiple, co-occuring insecticides in urban streams reported by Hoffman et al. (2000) indicates that insecticides are widely used in urban settings and similar effects on nontarget adults of aquatic insects are likely.

Research on the ability of aquatic insects to disperse has had varied results. Studies that have examined the movement of adult insects away from the stream generally have shown that most individuals stay close to or above the stream channel (Jackson and Resh 1989, Sode and Wiberg-Larsen 1993, Kovats et al. 1996, Collier and Smith 1998, Griffith et al. 1998, Petersen et al. 1999, Briers et al. 2002, Lynch et al. 2002, Petersen et al. 2004, Macneale et al. 2005, Winterbourn 2005, Chan et al. 2007, Winterbourn et al. 2007, Finn and Poff 2008). The rapid decline in abundance of adult insects caught with increasing distance into the riparian zone and upland areas has been interpreted as evidence that long-distance dispersal by adults is rare (Sode and Wideberg-Larsen 1993, Griffith et al. 1998, Petersen et al. 1999, Briers et al. 2002). However, studies of genetic relatedness among some aquatic insect populations suggest that long distance migrations across drainage basins are possible and even occur commonly (Hughes et al. 2000a, Kelly et al. 2001, Wilcock et al. 2001, 2003). Briers et al. (2004) labeled *Leuctra inermis* stoneflies (Plecoptera: Leuctridae) larvae with ^{15}N and were able to estimate that a small portion of adults migrated at least 1 km between streams. Kovats et al. (1996) used light traps and found inland movement by adult caddisflies up to 5 km from aquatic habitats. Light traps can artificially attract insects and, thus, might not represent typical dispersal distance, but these results show that long distance adult migrations on the scale of kilometers is physiologically possible. In addition, certain taxa can be passively transported long distances by wind (Kelly et al. 2001), especially those taxa, such as Plecoptera, that are weak fliers (Briers et al. 2004).

Observations that adult insects are most active over the stream channel often are interpreted as evidence that adults disperse between watersheds by traveling along stream corridors rather than in a direct path through upland areas. Petersen et al. (2004) and Sode and Wiberg-Larson (1993) collected more aquatic insects from traps placed across the stream channel than perpendicular to it, a result that suggested more individuals were flying above and parallel to the channel than away from it. Movement along the stream corridor can be extensive. Hershey et al. (1993) estimated that 33 to 50% of adult *Baetis* mayflies (Ephemeroptera) traveled 1.6 to 1.9 km upstream from where they emerged, and Coutant (1982) found ^{65}Zn labeled caddisflies up to 16 km upstream from the point source causing the radioisotope labeling.

In contrast, recent work has shown that adults can move between watersheds along a direct path through upland areas. Larval drift downstream past the confluence followed by adult flight upstream along the neighboring branch could result in the exchange of individuals between adjacent stream branches, but has not been proven (Griffith et al. 1998). In addition, the upstream bias of adult flight might prevent individuals from flying long distances downstream to a node and then up another branch (Macneale et al. 2005). The genetic structure of *Calopteryx splendens* (Odonata) damselfly populations along river networks observed by Chaput-Bardy et al. (2008) suggested that dispersal between watersheds by this strong flier occurs through upland areas rather than along networks, a pattern that might not be surprising for odonates. However, Macneale et al. (2005) found that dispersal patterns, dispersal distances, and capture rates of ^{15}N labeled adult *Leuctra ferruginea* stoneflies (Plecoptera) along the stream network indicated that individuals caught at an adjacent stream traveled through the upland areas to reach the adjacent stream rather than along the stream corridor, a result suggesting that size, strength, and flying ability are not the only determinants of cross-stream movement.

Urban Landscapes and Aquatic Insect Dispersal

Adult fitness

Terrestrial habitats altered by urbanization might be less hospitable than unaltered habitats to adult aquatic insects, and the alterations might directly affect adult development, survival, and mating success. In many geographic regions, riparian forests are important for adults of some species to complete development, feed, roost, and find mates (Sweeney 1993, Petersson and Hasselrot 1994, Smith and Collier 2000, Briers and Gee 2004, Winterbourn 2005). As such, riparian deforestation might impact adult development and mating success. In addition, the microclimate in remnant riparian patches might be altered by surrounding urbanization (e.g., a heat island effect; Oke 1989, Pickett et al. 2001). Collier and Smith (2000) found that adult stoneflies had lower mortality in forested habitats with lower temperatures and higher humidity than pastureland, and Jackson (1988) and Smith and Collier (2005) found that experimentally altered higher air temperatures decreased adult longevity for several aquatic insect taxa.

Deforestation of riparian areas also might lead to differences in types or abundances of natural enemies in urban landscapes and affect the level of predation on adult aquatic insects in remnant forest patches. Adult insects are important prey for animals, such as arachnids (Kato et al. 2003, Briers et al. 2005), birds (Gray 1993), bats

(Fukui et al. 2006), and lizards (Sabo and Power 2002). Predation in the terrestrial environment can contribute to significant mortality in adult aquatic insect populations (Gray 1989, Werneke and Zwick 1992, Paetzold and Tockner 2005). Urbanization often leads to an overall decrease in specialist predators and an increase in generalist predators in early successional areas recovering from the impacts of urban development (McIntyre 2000) and could increase predation on certain taxa. In general, altered mortality resulting from changes in predator communities is likely to have species-specific effects on aquatic insect populations depending on the species composition of predator assemblages (Paetzold and Tockner 2005) and individual species traits, such as adult life span (Jackson and Fisher 1986). For example, Faeth et al. (2005) found that increases in bird density and compositional shifts to more insectivorous species led to greater top-down control on herbivorous insect populations in urban areas than in the surrounding natural desert areas. In addition, greater top-down control was likely to occur with the conversion of other ecosystems to urban lands (Faeth et al. 2005). Increased predation on arthropods with increased urbanization is likely to decrease adult aquatic insect survival and decrease the probability of dispersing long distances among habitats.

Adult dispersal

Riparian deforestation and other changes to the riparian zone also might deter movement away from a natal stream (Sweeney 1993). Emigration frequently is triggered by environmental cues (e.g., wind speed or direction, light intensity, temperature or moisture gradients, presence or absence of trees or other vegetation) that can be altered or eliminated by urbanization (reviewed by Ims and Hjermann 2001). Harrison and Harris (2002) found greater diversity of aquatic insect adults in riparian areas with herbaceous vegetation and trees than in riparian areas consisting of grazed grasses. Collier et al. (1997) found a greater number of adult stream-insect taxa in native than in nonnative pine forests in the New Zealand hill country, and Smith et al. (2002) found a greater number of trichopteran species in native forests than in pasture land. However, factors affecting both larval community composition and adult dispersal in the aforementioned studies probably were controlling adult community composition. Winterbourn et al. (2007) found that adult Plecoptera, Ephemeroptera, and Trichoptera were more abundant in forested than in grassland habitat (although not significantly so for Trichoptera) and concluded that terrestrial habitat determined adult abundance in conjunction with larval distributions. Petersen et al. (1999) found that adult stoneflies were more abundant in the forested riparian zone than in the open riparian zone on the opposite side of the stream and clearly demonstrated the effect of terrestrial habitat type on adult dispersal.

For species that prefer to move through forested areas, migration among streams or reaches is subject to the location and distribution of forested patches. Adult dispersal can occur laterally through upland areas in intact forested watersheds (Fig. 1.2A), but might be limited to riparian corridors if upland areas are deforested (Fig. 1.2B). In watersheds with deforested uplands, increased dispersal distance among streams or reaches could increase energy use, risk of predation, desiccation, or encountering harsh habitats for migrating adult insects. Dispersal among streams might be constrained when both upland and riparian zones are deforested (Fig. 1.2C), but a natural affinity to stay above the stream might allow dispersal along the stream corridor.

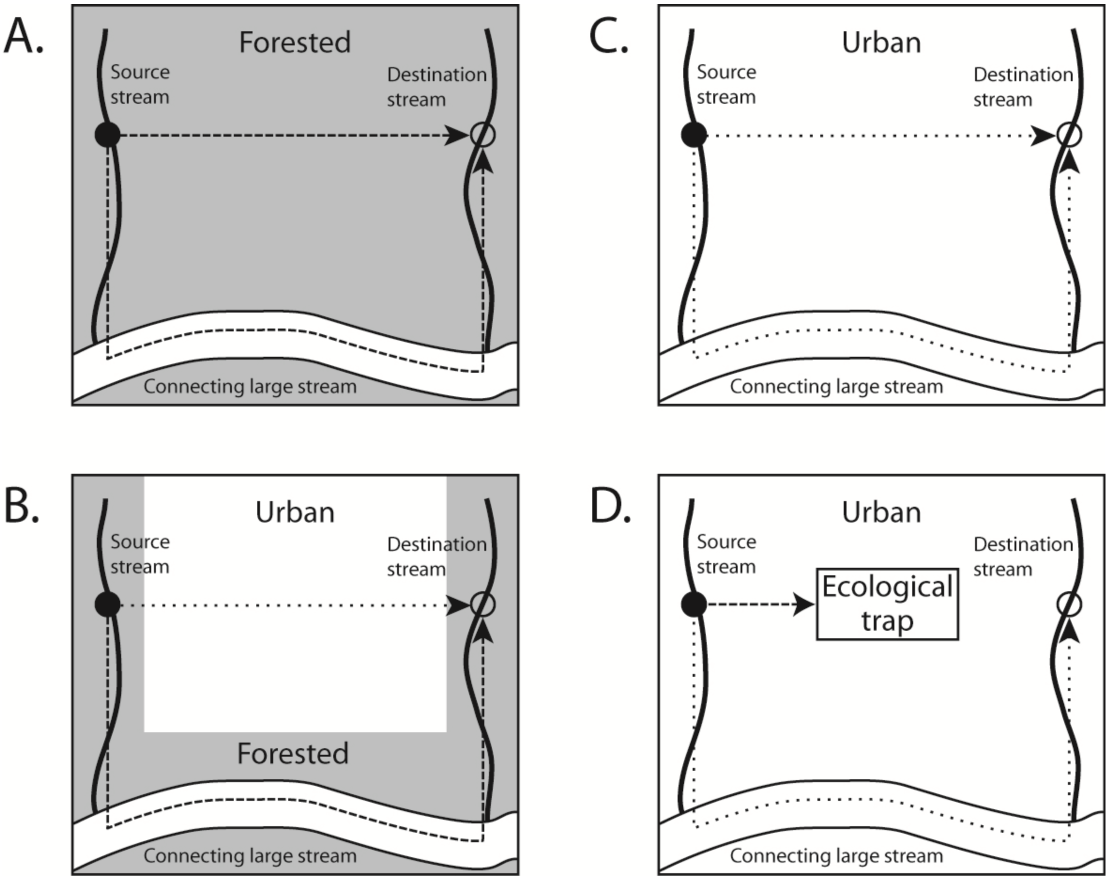


Fig. 1.2. Diagram showing how transport between 2 adjacent headwater stream reaches flowing into a larger, main-stem stream could be affected by the loss of forested areas (shaded) in association with urbanization (unshaded). A. - Upland and riparian zones are forested and dispersal is not impeded. B.–Upland areas are deforested, but riparian zones remain forested. C.–Upland and riparian zones are deforested. D.–Upland and riparian zones are deforested and ecological traps, attractive to adult insects, exist in upland areas. Closed circles indicate the source of adults and the open circles indicate the destination. Dashed lines indicate a more likely pathway of dispersal and the dotted lines indicate a less likely pathway of dispersal.

Preference of some taxa to move into forested areas might not always translate into a greater amount of adult migration in forested than in open riparian and upland areas. Briers et al. (2002) found that whether an open riparian area discouraged, encouraged, or had no effect on movement away from the stream compared to a forested riparian zone depended on individual species. Furthermore, Delettre and Morvan (2000) found that chironomid flies tended to aggregate in vegetated areas rather than open areas near the stream, and as a consequence, isolated riparian forests surrounded by deforested watersheds actually might have discouraged emigration because insects were less likely to move from the preferred forested habitats into open habitats to migrate to another stream (Delettre and Morvan 2000). The tendency to seek forested habitat observed by Delettre and Morvan (2000) also might cause adult insects in open habitats (e.g., Fig. 1.2C) to disperse further to seek forested habitat. Higher temperatures from loss of riparian vegetation might decrease survival (Jackson 1988, Collier and Smith 2000, Smith and Collier 2005), but also might lead to greater flight activity (Briers et al. 2003) and potentially increased transport distances on short time scales for individuals in warm, deforested habitats. Thus, the actual effect of riparian vegetation on emigration is complex and requires further study.

The loss of natural structures from and the addition of anthropogenic structures to watersheds also can affect dispersal (Fig. 1.2D). Insect species that use highly specific stream or riparian structures as swarming markers (Savolainen et al. 1993, Tokeshi and Reinhardt 1996) or species that prefer shaded conditions (Petersson 1989) might fail to remain at urban streams with simplified or artificial habitat conditions. Other taxa are at risk of encountering anthropogenic structures or areas in urban landscapes that attract individuals but are inhospitable to them or their offspring (i.e., ecological traps; Kristan 2003; Fig. 1.2D). For example, adults of many aquatic insects use polarized reflected light to locate aquatic habitats (Bernáth et al. 2002) and anthropogenic structures that reflect polarized light can attract dispersing aquatic insects (Horváth and Varjú 1997). The reflective surfaces of cars mimic the polarization of reflected light from streams, and as a result, parking lots are potential sinks for migrating insects in urban watersheds (Kriska et al. 2006). Asphalt and other road surfaces, which have a shape similar to that of streams, also reflect polarized light and attract mating swarms of mayflies (Kriska et al. 1998) and midges (Tokeshi and Reinhardt 1996). Other structures, such as glass buildings (Kriska et al. 2008) and black gravestones (Horváth et al. 2007), that reflect polarized light also have been identified as potential attractants of aquatic insects. Street lights might act as ecological traps for phototactic species dispersing at night (Eisenbeis 2006), but few studies have examined their impact on aquatic insects. The use of mercury vapor lamps and black lights by entomologists for nighttime trapping is proof that artificial lights can attract adult aquatic insects.

In contrast to ecological traps that can attract adult insects, some anthropogenic structures can block movement of adult aquatic insects. Impediments above the stream, such as culverts, might block movement of adult taxa flying upstream (Blakely et al. 2006). In contrast, structures, such as bridges and low head dams, are less likely to affect dispersal along streams (Blakely et al. 2006, Grenouillet et al. 2008). Roads and bare ground are sometimes barriers to ground (Mader et al. 1990) and aerially (Lövei et al. 1998) dispersing terrestrial arthropods. In general, few studies have demonstrated the potential for anthropogenic structures in upland areas to act as physical barriers to aquatic insect movement and could be an area of future study.

Habitat Fragmentation

Taxa respond differently to habitat loss and fragmentation, but general patterns (reviewed by Ewers and Didham 2006) include lower population size, increased demographic stochasticity, reduced levels of gene flow, loss of genetic diversity (Watts et al. 2004), and increased risk of extirpation or extinction (reviewed by Fahrig 2003). Degradation of matrix habitat can lead to spatial isolation of populations by impairing dispersal (Ricketts 2001). Degradation of the matrix of dendritic stream networks occurs when upland and riparian zones between stream reaches are altered (Grant et al. 2007). The combined effects of aquatic and riparian habitat loss can contribute to spatial isolation of populations by eliminating populations from the landscape and increasing the distance between suitable habitats (Lowe 2002). Thus, the effects of fragmentation might be particularly relevant to adult aquatic insect populations in headwater streams. If remnant and restored forest patches are limited to the riparian zone, formerly 2-dimensional forests (Fig. 1.2A) are reduced to 1-dimensional dendritic networks that follow stream corridors (Fig. 1.2B). The resulting dendritic forests might interact with the behaviors of flying stream insects (e.g., the propensity to aggregate or move into forested areas) to impose new constraints on dispersal, with consequences for population persistence. Dendritic habitat structure alters the dispersal, isolation, and population extinction probabilities of taxa (e.g., fish, salamanders) that move only within or along such networks (Lowe 2002, Fagan 2002, Fagan et al. 2005, reviewed by Lowe et al. 2006, Grant et al. 2007). In contrast, emergence as winged adults in fully forested watersheds permits insects to leave the channel and to move among stream habitat patches, unconstrained by the network's hierarchical structure. Thus, even when riparian zones are intact, upland habitat alteration can isolate populations or patches within a stream network by imposing novel spatial constraints on terrestrial dispersal.

In addition to riparian corridors, habitat fragmentation that restricts terrestrial dispersal might be particularly important for populations in headwater streams. Headwaters often have unique habitats with assemblages of endemic insect populations (Gomi et al. 2002, Finn et al. 2007, Gooderham et al. 2007, Meyer et al. 2007, Richardson and Danehy 2007, Clarke et al. 2008, Smith and Lamp 2008, but see Heino et al. 2003a, 2005). Dispersal into headwaters is limited to flying adults because no upstream sources of stream residents are available from drift. As a result, the unique characteristics and location of headwaters in stream networks might contribute to natural isolation. Conversion of headwater streams to buried underground drainage systems in urban watersheds and the loss of ephemeral and intermittent headwaters caused by altered hydrology (Elmore and Kaushal 2008, Roy et al. 2009) can increase the isolation of headwater populations by eliminating headwater habitat and increasing the distance among remaining populations in urbanized watersheds. As a result, the headwater populations in urban watersheds might be connected only to populations in the adjacent main-stem stream (Smith and Lamp 2008). Thus, headwaters might experience even greater isolation from fragmentation in urban watersheds than larger streams.

Interaction with species traits

The interaction of species' characteristics (e.g., habitat specificity, dispersal ability) and landscape properties (e.g., physical obstacles, loss of habitat) can determine the extent to which aquatic insect populations are affected by fragmented urban environments. Species traits, such as larger overall size, greater thoracic mass, greater wing loading, and greater wing size, are related to greater population range sizes (Malmqvist 2000, Hoffsten 2004, Rundle et al. 2007) and flight ability (Rankin and Burchsted 1992, Marden 2000, Berwaerts et al. 2002). These traits also might be correlated with a greater ability to avoid or withstand harsh terrestrial habitats in urban watersheds, but to our knowledge, this possibility has not been examined. However, Sato et al. (2008) detected greater population genetic structure (but no significant loss of genetic diversity) in 3 highly mobile damselfly species in urban than in rural ponds in Japan. Even though this study examined lentic species, population differentiation was greatest in the species with the most specific habitat requirements and indicated that population fragmentation is dependent on species traits in addition to dispersal ability (Sato et al. 2008).

Interspecific differences in dispersal ability might result from adaptations to specific habitats and thus be associated with species-specific affinities for certain habitat types. Thus, any decrease in colonization potential in urban watersheds results from a complex interaction between the type of habitat affected by watershed urbanization and the preferred habitat and dispersal ability of the insect species. For example, Wilcock et al. (2007) compared the genetic structure of 2 species of caddisflies in streams and found that *Plectrocnemia conspersa* (Trichoptera:Polycentropodidae), which inhabits smaller intermittent streams, dispersed more than *Plectrocnemia flavomaculatus* (Trichoptera:Polycentropodidae), which inhabits larger perennial streams. Selection for strong dispersal ability in headwater taxa adapted to living in intermittent habitats might allow these taxa to persist longer in urban landscapes than poorer dispersing taxa adapted to living in more permanent, large streams (Wilcock et al. 2007). However, loss of small, intermittent streams in urban watersheds (Elmore and Kaushal 2008) could mean that those species adapted to greater dispersal have no habitat to colonize in urban watersheds.

Applications

Data on terrestrial stages, life-cycle processes, species traits, and adult dispersal of aquatic insects are difficult to obtain, but might be necessary to identify the mechanisms by which populations lack persistence in urban streams. Moreover, interactions among species traits, landscape variables, and specific human impacts might be difficult to observe, and even more difficult to relate to different life stages. Life-history, dispersal, morphological, and ecological traits are being used to explain larval presence/absence in urban streams and to predict community composition in streams (Poff et al. 2006, Horrigan and Baird 2008, Statzner et al. 2008, Verberk et al. 2008). Incorporation of species traits into these types of studies would further enhance restoration and conservation initiatives.

Restoration

Success of community redevelopment in stream restoration projects depends on the ability of species to disperse to and recolonize restored stream ecosystems (Palmer et al. 1997, Bond and Lake 2003, Lake et al. 2007). The potential for long-distance dispersal across terrestrial habitats makes aquatic insects likely candidates to colonize restored streams (Hughes 2007) as is evidenced by Masters et al. (2007), who found 8 species of acid-sensitive Ephemeroptera, Plecoptera, and Trichoptera adults beside acid streams where larvae had not observed in 21 y of benthic sampling. Some investigators assume that flight-capable insects have extensive enough dispersal that restoration of local habitat should be the focus of restoration and that restored local habitat is sufficient to promote recolonization and community development (Palmer et al. 1997). However, recolonization is controlled by: 1) species life-cycle and dispersal traits, 2) the spatial structure of source populations, stream networks, and remaining urban land use, and 3) the temporal patterns of project completion and the interactions among them (Mackay 1992, Palmer et al. 1997, Bond and Lake 2003, Lake et al. 2007). Identifying and conserving dispersal pathways could help mitigate the effects of urbanization on stream insect communities and encourage dispersal (Lowe 2002), but doing so will require a better understanding of the adaptive behaviors of species to past and present spatial structures of stream ecosystems and of how differences in the matrix affect dispersal and movement of individuals in fragmented stream systems (Ricketts 2001, Davies et al. 2001).

Predicted outcomes and assessments of stream restoration projects probably would improve if species traits, spatial population structure, dispersal pathways, and spatial characteristics of stream networks were considered during project design (Jansson et al. 2007, Lake et al. 2007, Spänhoff and Arle 2007). The slow recovery of communities in urban environments with constrained dispersal also might require adjusting the timeline for determining the success of restorations of aquatic insect communities (Lake et al. 2007). Ideally, assessments of restoration success should consider potential dispersal limitations when bioassessments based on aquatic insects are used (Purcell et al. 2002). Surveys of potential source populations might be helpful because the probability of colonization increases with a greater number of and a shorter distance to source populations (Fuchs and Statzner 1990, Huxel and Hastings 1999, Ahlroth et al. 2003). Loss of source populations, rather than failed restoration of local habitat, could be the reason a species fails to recolonize a restored reach (Suding et al. 2004). Urban stream restoration methods also might have to address specifically the impacts to life-cycle process that are responsible for species loss. Even more radical approaches, such as stocking insects into restored streams, might be possible when recolonization is unlikely, but research is needed on this approach (Brady et al. 2002). However, we think that managers should not simply give up on restoring streams in situations where dispersal is severely impeded and colonization is unlikely. In situations like this, designers of assessments of restoration success might find using direct measures of functional and geomorphological attributes of stream health more practical and more informative than using bioassessments based on stream insects.

Framework for identifying stage-specific urban effects

Estimates of movement of adult aquatic insects from one stream to another are difficult, generally require expensive methods to label individuals (but see Payne and Dunley 2002) or sequence genetic samples, and often are impractical to include in assessments of impacts from urbanization. Surveys that use malaise traps, light traps, or sweep nets can provide some estimate of dispersal ability and presence/absence, but do little to indicate actual levels of movement among habitats (Macneale et al. 2004). In lieu of these approaches to measuring dispersal, patterns of adult and larval presence/absence can be used to determine how impacts to terrestrial stages are influencing population persistence in urbanized streams.

Table 1.1 illustrates how surveys of aquatic larvae and terrestrial adult populations in different habitat types within a region can help to identify potential mechanisms that are linked to population dynamics. In this case, we consider populations in urban and rural headwater streams. Each line represents a presence/absence scenario and a potential mechanism based on the assumption that dispersal between the 2 habitats is possible. We think the mechanisms that structure larval communities in urban headwaters can be grouped into 2 categories: 1) mechanisms that influence population dynamics of tolerant larval taxa able to survive in urban headwaters and 2) mechanisms that lead to and maintain the absence of larval taxa from urban headwaters. The 1st category includes species that occupy urban headwater streams as larvae and, by default, are found there as adults (scenarios 1, 4, and 7, Table 1.1). These taxa usually are tolerant of habitat degradation and are able to complete their life cycle. If adults do not emerge from the natal stream then recruits from adult immigrants rescue the population (e.g., source–sink dynamics; Caudill 2003).

(Table 1.1 - Caption)

Table 1.1. Potential mechanisms controlling species presence/absence from the focal habitat (in this example, an urban headwater) for various combinations of species presence/absence in the regional species pool for the focal habitat and in the focal habitat itself. This framework is a starting point for hypothesis generation and further investigation and includes only relevant presence/absence scenarios. Species with low abundances might be rare and undetected by surveys.

(Table 1.1 – table)

	Present in regional pool of similar habitats? (e.g., rural headwaters)		Present in focal habitat? (e.g., urban headwater)		
Scenario	Larvae	Adults	Larvae	Adults	Possible mechanisms affecting presence/absence in the urban headwater
1	Yes	Yes	Yes	Yes	Species is ubiquitous and able to survive in poor habitat or larval mortality rescued by adult immigrants (i.e., source–sink dynamics).
2	Yes	Yes	No	Yes	Immigration of adults occurs but poor habitat prevents successful reproduction (mating and oviposition) or causes egg or early instar mortality to prevent detection.
3	Yes	Yes	No	No	Immigration of adults does not occur. (Note: mechanisms in scenario 2 above may occur if immigration restored)
4	No	Yes	Yes	Yes	Species tolerant of poor habitat. (Source–sink dynamics possible)
5	No	Yes	No	Yes	Species not suited for this habitat (not a headwater or stream species). (Mechanisms in scenario 2 above might occur, but less likely)
6	No	Yes	No	No	Immigration of adults does not occur. (Mechanism from scenario 5 might occur if immigration occurs)
7	No	No	Yes	Yes	Species tolerant of poor habitat. (Source–sink dynamics possible)
8	No	No	No	Yes	Species not suited for this habitat (not a headwater or stream species). (Mechanisms in scenario 2 might occur, but less likely)

The 2nd category includes species whose larvae occupy rural headwater streams but are absent from urban headwater ecosystems (scenarios 2 and 3, Table 1.1). This category is of greater interest for determining if impacts on adults lead to the persistent loss of populations from stream communities and for determining the potential for the community to return following restoration. Scenario 2 (Table 1.1) indicates that dispersal barriers are not likely to lead to the absence of larvae because adults of that taxon can migrate to the reach, so high egg mortality, some barrier to successful mating, or a lack of oviposition sites or cues are the cause of larval absence. High mortality of early instar larvae also might result in an apparent absence of larvae from the stream community. Presence of even 1st-instar larvae generally is representative of scenarios 1, 4, and 7. High mortality of early instars generally has the same effect as high egg mortality and should be considered in the presence or absence of scenario 2. The pattern in scenario 3 (Table 1.1) indicates that a dispersal barrier is present, and that a lack of adult immigrants was partly responsible for the lack of colonists. However, some effect occurring in the stream (e.g., early instar or egg mortality) or at the terrestrial/stream interface (e.g., preventing oviposition) cannot be ruled out and could result in a lack of colonists even if migrants arrived. The mechanisms are not definitively identified from this conceptual model, but the patterns of adults and larvae could be useful for resource management and restoration activities.

Comparing adult and larval presence/absence (Masters et al. 2007) and the interaction between regional- (e.g., dispersal) and local-scale processes that affect population dynamics (Palmer et al. 1996) is not a novel idea. The model in Table 1.1 is a simple framework for identifying how local and regional processes can affect communities. Collecting data on adult presence/absence can reveal the occasional movements of adult individuals over long distances that probably are important for population rescue and persistence (Bunn and Hughes 1997, Macneale et al. 2005). Only a few studies have experimentally examined the conditions under which regional or local processes are the more important regulators of community structure for stream insects (e.g., Sanderson et al. 2005) or how pre- and postrecruitment processes drive population dynamics (e.g., Peckarsky et al. 2000, Reich and Downes 2004).

Local processes important for colonization include more than just the survival of larval stages. Specific structures often are required for pupal attachment (Hoffmann 2000), emergence (Petersen and Hildrew 2003, Jáimez-Cuéllar and Tierno de Figueroa 2005), oviposition, or egg attachment (Hoffmann and Resh 2003, Lancaster et al. 2003, Reich and Downes 2003a, b, Encalada and Peckarsky 2006). Changes to stream geomorphology and hydrology that result from watershed urbanization might eliminate these physical factors. Elimination of structures might present a barrier to colonization, but evidence that only a few individual adults are responsible for most recruits (Bunn and Hughes 1997) and that larval density (Reich and Downes 2004) and emergence density (Peckarsky et al. 2000) are unrelated to oviposition site abundance suggests that limited availability of oviposition sites might not necessarily be a barrier to recruitment. Regardless, the framework we present still allows potential identification of terrestrial (i.e., limited migration) and aquatic effects, which include the rest of the insect’s life cycle (oviposition to emergence).

Conclusions

Urbanization probably hinders completion of life cycles in terrestrial habitats and constrains adult dispersal of stream insects, but the specific effects of urbanization on population demography and dispersal are relatively understudied (Strayer 2006). We recommend that future studies of stream urbanization incorporate new strategies that differ from the traditional focus on larval stages and instream effects to confront confounding aquatic and terrestrial effects on population persistence. We presented an approach to provide a starting point for determining the role of specific life-cycle stages or processes for insect population dynamics in urbanized streams. However, further work is required to define and quantify changes to terrestrial habitats that have negative consequences for adult insect fitness and dispersal. Areas that require new or continuing work include: 1) understanding dispersal patterns of adult aquatic insects in urban watersheds, 2) identifying dispersal barriers and ecological traps affecting movement of adult aquatic insects in urban environments, and 3) understanding the long-term consequences of changing landscapes on population genetics and species persistence. In addition, these studies should be conducted in a variety of urban ecosystems (e.g., deserts, coniferous forests, subtropical and temperate regions). An understanding of how watershed urbanization affects terrestrial life stages and adult dispersal will lead to a better understanding of anthropogenic activities that affect stream insect populations, conservation measures that might help preserve populations, and restoration methods to improve urban stream structure and function.

Chapter 2: Spatial and temporal patterns of abundance and richness of the adult caddisfly (Trichoptera) assemblage at urban and rural headwater streams

Abstract

Life stages of species with complex life cycles often differ in the spatial scale that they interact with their environment. The ontogenetic shifts in the environmental requirements can cause the overall mechanisms controlling population and community dynamics to operate at multiple spatial scales. Community and population level studies of insect fauna in urbanized streams generally focus on the mechanisms associated with the larval stages operating at a scale within the stream. Decreased survival and dispersal experienced by the adult stage at large spatial scales in urbanized terrestrial landscapes can also have important impacts on overall population and community dynamics. The objective of this study was to investigate the effect of urbanization on the spatial and temporal patterns of adult caddisfly abundance and species richness. I hypothesized that patterns of abundance and richness varied between urban and rural headwater streams. Caddisfly adults were sampled using Malaise traps at 4 urban and 4 rural headwaters during 10 sampling periods from March to November, 2010. Total caddisfly abundance and abundance through time generally did not differ between urban and rural headwaters, but total richness and richness at 6 of the 10 sampling periods were greater at rural than urban headwaters. Peak abundance times only differed between urban and rural streams for one species of caddisfly. Female:male sex ratios were not significantly different between urban and rural streams, and a female bias was generally found across all streams for the species analyzed. Poor quality aquatic and terrestrial environmental conditions resulting from land use urbanization likely caused lower adult richness at urban streams. High production by larvae residing in urban streams may have resulted in high abundances of the few taxa of adults observed at urban headwaters. Changes to the adult caddisfly assemblage resulting from land use urbanization may not impact assemblage-wide reproductive potential, but a clear decrease in taxa richness occurred at urban headwaters.

Introduction

The processes of reproduction, dispersal, and resource accumulation for species with complex life cycles are often distributed between specific life stages that experience ontogenetic shifts in habitat preference, susceptibility to predation, or energy requirements (Wilber 1980, Werner and Gilliam 1984). Activities associated with these processes are important for population persistence and abundance, and any factors that alter fitness of the stages that include these processes may control recruitment and other demographic processes (Roughgarden et al. 1988, Beck 1995). Thus, impacts to one life stage may determine the population abundance or assemblage composition of other life stages (Wilber 1980). I investigated the spatial and temporal differences of population and assemblage level characteristics of adult caddisflies in human-impacted and natural landscapes to determine the response of the reproductive stage to land use urbanization.

The spatial and temporal patterns of abundance of the reproductive stage are particularly important for recruitment and population persistence. Environmental factors affecting survival and dispersal of the non-reproductive stage can partly determine recruitment by controlling population size and the geographic location of populations (Stoeckel et al. 1997). A lack of reproductive output resulting from low abundance of the reproductive stage can directly limit recruitment by restricting the number of offspring produced (Hughes et al. 2000b). Factors affecting recruitment for each life stage may have independent or interacting effects on the overall population when individual life stages interact with the same environments (Lowe et al. 2004). In addition, movement of reproductive individuals between habitats may offset limitations on population growth experienced by local populations of the non-reproductive stage (i.e., source sink dynamics) (Dias 1996). Temporal patterns of abundance of and dispersal patterns by reproductive stages also control synchrony of populations across habitat patches, and asynchrony of populations at small abundance levels may decrease reproductive output (Calabrese and Fagan 2004).

The processes controlling population and community dynamics differ between developmental stages when the stages interact with the environment at different spatial scales (Heino et al. 2003b). Sedentary stages are impacted only by local environmental conditions, and dispersing stages are impacted by both local environmental conditions and characteristics of the landscape. The interaction of abundance and dispersal patterns resulting from direct impacts to each stage controls demographic processes and population persistence (Roughgarden 1989). Thus, mechanisms operating at small and large spatial scales may influence population and community dynamics by impacting the life stages that are most associated with each spatial scale. Bottlenecks to population persistence occur from species-specific environmental requirements (Beck 1995), which may differ between life stages. At the landscape scale, regional richness sets the upper limit for local species richness (Heino et al. 2003b). Landscape-scale features that control dispersal determine which species from the regional pool are able to colonize specific patches, and colonization is based on local habitat conditions and species traits (Poff 1997, Ricketts 2001).

Human activities may alter the landscape scale processes controlling the movement of dispersing stages (Fahrig 2007), and the demographic changes resulting from these changes may contribute to changes of community composition. Land use change for human needs generally results in increased fragmentation and altered environmental conditions within and between habitat patches (Pickett et al. 2001, Elmore and Kaushal 2008). These changes can decrease dispersal, which may alter alpha and beta diversity of communities remaining in isolated habitat patches (Urban et al. 2006).

The different life history processes and habitat preferences associated with adult and larval stages of stream insects alter how environmental factors affect population dynamics. The adult stage of stream insects includes the life history processes of reproduction and dispersal, but resource acquisition only occurs during the larval stage. Stream insect adults are generally most closely associated with the terrestrial environment while stream insect larvae are confined to the aquatic environment. While the adult stage is generally short lived, environmental factors in the terrestrial environment such as predation (Sabo and Power 2002, Paetzold and Tockner 2005), microclimate (Collier and Smith 2000), and habitat (Sweeney 1993, Petersen et al. 1999) may have substantial impacts on population size, which can influence population and community dynamics for all stages.

The majority of studies on abundance patterns of adult stream insects have focused on the colonization cycle (or generally on the preference for upstream flight) (Hershey et al. 1993, Winterbourn and Crowe 2001), movement patterns of males versus females (Petersen et al. 1999), abundance patterns related to riparian or upland habitats (Petersen et al. 1999, Petersen et al. 2004), and abundance patterns related to distance away from the stream channel (Sode and Wiberg-Larsen 1993). The most common result from these studies is that abundance of adult steam insects is greatest over the stream channel and decreases quickly into the riparian zone.

Studies on the differences in spatial and temporal abundance patterns of adult stream insects between natural and urban landscapes are generally lacking (except see Purcell et al. 2002). The deficiency of research on adult stream insects in urban stream ecology exists despite the importance of the adult stage for reproduction and dispersal and the potentially substantial decrease in the fitness of adult stream insects in urban landscapes (chapter 1). Impacts to the adult stage may alter demographic processes and decrease population persistence, which can lead to the loss of diversity. Altered emergence date due to warmer temperatures in urban streams (Paul and Meyer 2001) or altered temporal abundance patterns of adults due to mortality in urban terrestrial landscape (chapter 1) may interact with constrained dispersal to cause asynchronous population abundances through time and decreased reproductive potential (Calabrese and Fagan 2004). Altered sex ratios may also result from altered in-stream and terrestrial habitat in urban areas, but the possibility that only a few adult females are responsible for the majority of larval recruitment (Bunn and Hughes 1997) may make altered sex ratios unimportant for population persistence.

The goal of this study was to investigate spatial and temporal patterns of abundance and composition of adult trichopteran assemblages between urban and rural headwater streams to characterize the trichopteran assemblage's response to landscape urbanization. Inter-site differences in abundance and composition of the adult assemblage are obviously linked to abundances of larvae found locally in the stream, and an analysis of differences in community composition between urban and rural streams is done in chapter 3. The specific objectives for this chapter included to determine if: 1) overall abundance and richness, 2) assemblage and population peak abundance patterns, and 3) female:male sex ratios at the assemblage and population levels differed between urban and rural streams. I hypothesized that caddisfly abundance and richness across all sample periods and for individual sample periods were lower at urban that rural headwaters. I hypothesized that peak abundance times for the entire assemblage and for individual taxa were earlier at urban that rural streams. I also hypothesized that sex ratios for males and females differed between urban and rural headwater streams. Given the lack of studies focusing on adult stream insects in urban settings, I also briefly discuss the effectiveness of the sampling protocol for collecting adult Trichoptera from urban streams examined in this study.

Methods

Study organism and life cycle

Caddisflies are a holometabolous aquatic insect found in many Maryland headwater streams. Taxa within this order vary in their tolerance of pollution, and different taxa are found along a gradient of human disturbance. In addition, certain species may inhabit both undisturbed (i.e., rural) and disturbed (i.e., urban) streams. Life-history characteristics vary among taxa within this order, and functional feeding groups assigned to larvae within this order include collector-filterers, collector-gatherers, predators, and scrapers (i.e., algal eaters) (Wiggins 2004, Morse and Holzenthal 2008). Previous work identified 21 taxa (genera and species) of larval Trichoptera at 3 urban and 3 rural headwater streams and their associated main-stem reaches in Maryland's piedmont (Smith 2006). Preliminary work found that adult Trichoptera were efficiently sampled at urban and rural headwater streams using Malaise traps (Appendix B).

Study area / stream selection

All study streams were located in the Piedmont physiographic province of Montgomery and Carroll counties, Maryland, USA (Fig. 2.1). Smith et al. (2009) characterized the Piedmont as having "rolling terrain" that includes stream channels cut by erosion, often occurring in valleys, and usually with moderate slopes (though steep slopes do exist for some tributaries). Sampling was done at 4 urban and 4 rural headwater streams for a total of 8 study streams. For this project, a headwater was defined as a first order reach with no permanent tributaries (see Meyer et al. 2003 for general definition of a headwater stream). Potential stream locations were selected by examining USGS topographic maps and local street maps for headwater streams based on access, size, and location. All candidate streams were then analyzed for percent urban land use in the watershed with a goal of greater than 75% urban land use for "urban" streams, and less than15% urban land use for "rural" streams. Urban land use was defined as any residential, commercial, or industrial land use. Watershed land use

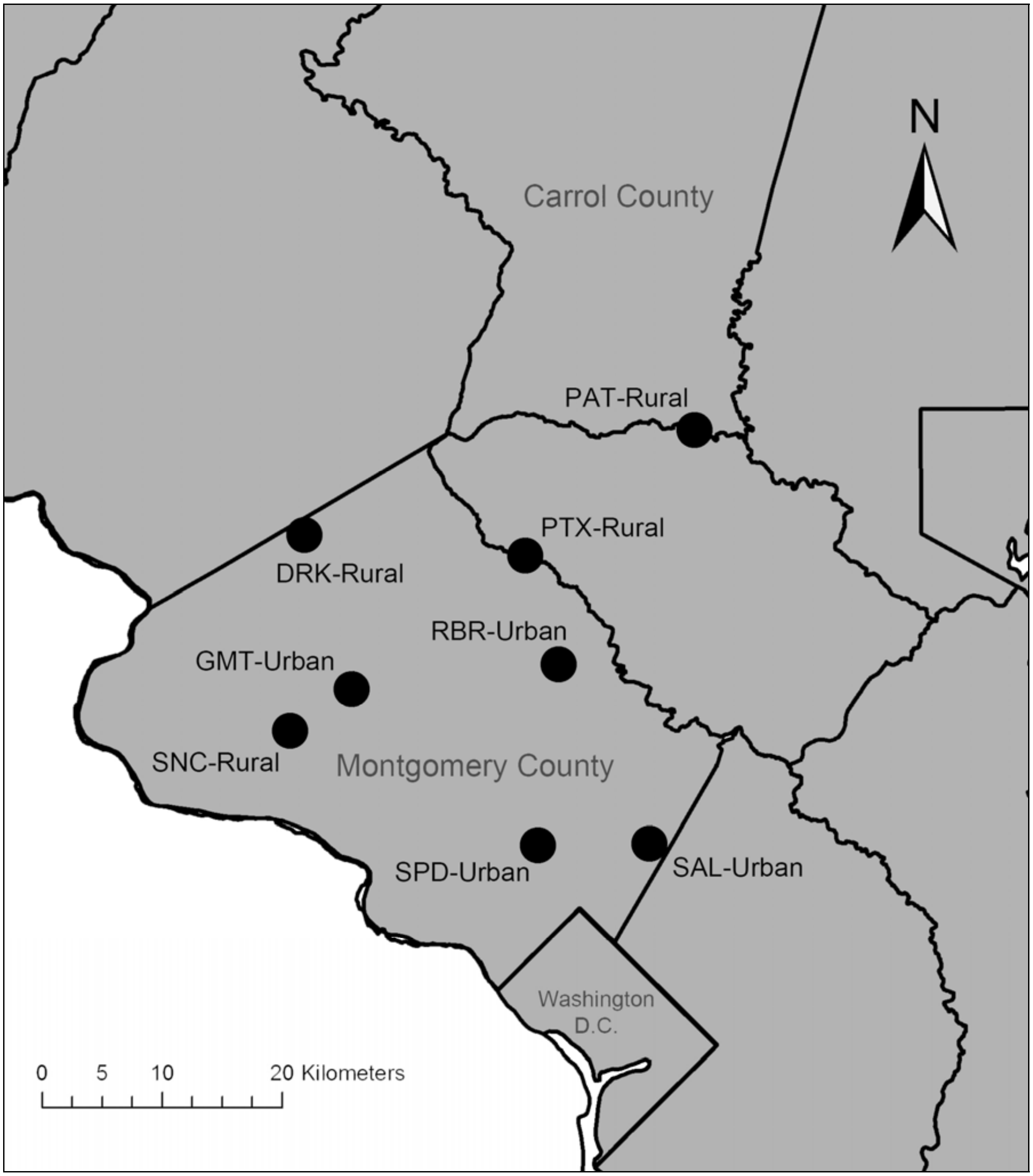


Fig. 2.1. Map of headwater stream locations sampled for adult caddisflies. Streams were in Montgomery and Carroll counties of Maryland's Piedmont region.

statistics for stream selection were calculated with Maryland Department of Planning geographical information system (GIS) land coverages (30-m resolution) available in the ArcView (version 3.3; Environmental Systems Research Institute, Redlands, California) supplement program GISHydro2000 (2nd edition; Department of Civil and Environmental Engineering, College Park, Maryland; Moglen 2005). Candidate streams were visited to determine if the stream met the criteria for a headwater as defined for this study and to determine the feasibility of working at the location. The site selection procedure resulted in 4 urban and 4 rural headwater streams used in this study (Fig. 2.1).

Field collections

Adult caddisflies were collected at 2 locations along each headwater stream using Malaise traps for a total of 16 malaise trap locations along all 8 streams (Fig. 2.2). Collections were made at a downstream location and an upstream location along each headwater. The downstream location at 100m from the mouth of the headwater was determined by manually measuring the distance upstream from the mouth. The upstream location at a distance of 75% of the total stream length was based on estimates from Google Earth with knowledge of the stream's origin from preliminary visits to each stream (Table 2.1). Streams originated from discrete locations such as stormwater pipes, permanent ponds, (including stormwater retention basins), or an agricultural tile drain (Table 2.1). Malaise traps were hung from frames attached by ropes to trees in the riparian zone. The actual location of the trap at up and downstream locations varied based on the locations of suitable trees across the stream from each other, which were required to situate traps with their middle baffles perpendicular to the stream channel (Fig. 2.2). If the exact location was not suitable, the closest location up or downstream was chosen. Traps were also not placed directly next to large anthropogenic structures (e.g., bridges), large debris dams, or other structures that could block movement into the traps and bias the catch.

The Malaise traps used were Townes style traps that differed from the traditional design by collecting specimens from each side of the trap into individual collection jars. Traps were purchased from Sante Traps (Lexington, KY); and each was constructed with all black 0.33mm mesh, had a 10cm black cloth strip along the top edge of the opening on each side, and collected specimens into 500ml plastic bottles (Fig 2.2). The openings on both sides of the trap were 1.2m height on the front (i.e., side with the collecting head), 0.9m height on the back, and 1.7m wide (Fig. 2.2). The traps' perpendicular orientation to stream flow was used to collect individuals moving parallel to and above the stream channel at the time of capture and those that fly skyward after emerging directly below the trap. Preliminary work showed that traps placed above the stream channel and perpendicular to flow were more efficient at collecting caddisflies than traps on the bank oriented parallel to flow (Appendix B). Traps were set up so the bottom of at least one side of the trap was at the water's surface. Suspending the traps so the bottom was level with the water's surface was difficult due to topography of the stream bank and the structure of the stream bed at each location. While gaps at the bottom of the traps could have limited the capture of species that fly close to the water's surface, the gaps between either side of the bottom and the surface of the stream were generally small (less than 20cm at the time of deployment) and likely did not bias the catch. Trap height was adjusted during each collection visit as water levels rose and fell throughout the year.

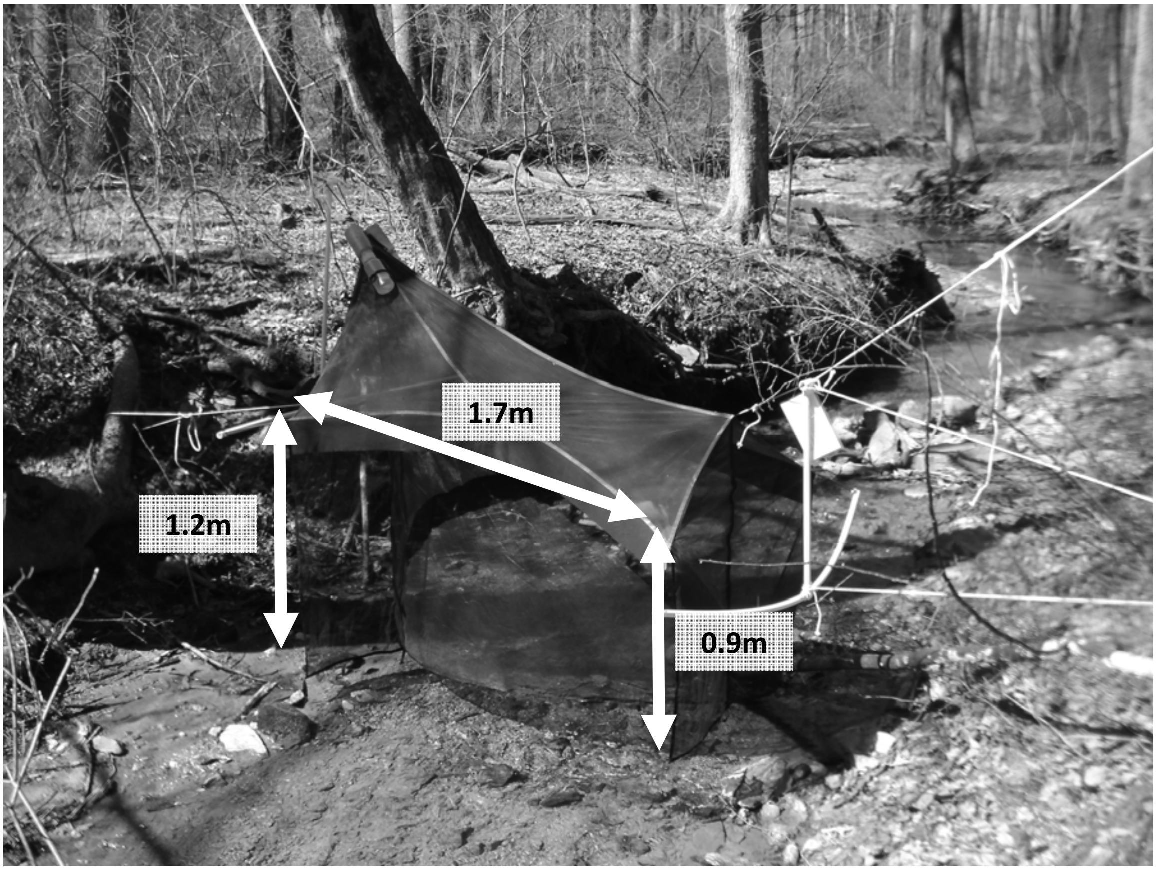


Fig. 2.2. Photograph of a Malaise trap demonstrating its position perpendicular to stream flow. Each trap was suspended from PVC frames tied to trees in the riparian zone. Dimensions of the trap opening are noted in the picture.

Table 2.1. Information on sample site location and stream size.

	Site	Origin	Dist. from mouth to downstream site (m)	Dist.from mouth to upstream site (m)	% of total stream length to upstream site	Discharge (m^3/s)
Rural	DRK	Pond	110	1195	69%	0.0257
	PAT	Pond	136	882	67%	0.0103
	PTX	Tile drain	118	993	68%	0.0088
	SNC	Pond	157	1577	69%	0.0310
Urban	GMT	Pond	211	1395	77%	0.0345
	RBR	Pipe	223	1524	71%	0.0196
	SAL	Pipe	121	490	77%	0.0036
	SPD	Pipe	93	255	70%	0.0037

Malaise traps were deployed March 15-27, 2010 and collections ended on November, 16-17 2010 (Table 2.2). Samples were collected from weeks 1, 2, 6, 10, 14, 18, 22, 26, 30, 34 following deployment (Table 2.2), which resulted in 10 samples from each stream. Each sampling period will be referred to as a “week” for this dissertation even though actual sample times were not always 7 days. Trap deployment occurred prior to or at the start of collections for week 1, and total catch times differed between streams based on the date that traps were deployed (Table 2.2). Week 1 was included to ensure that caddisfly taxa present only during the spring were included in the analysis. Trap deployment was delayed until March due to record snowfall that occurred in the region during February that made Malaise trapping impossible. Week 2 was the first sampling period that included similar deployment times across all streams. Starting at week 2, collections were done on a weekly basis with 4 sites visited on each of 2 separate days every 6-8 days. The traps at stream PTX for week 22, however, were collected after only 5 days (Table 2.2). The order for visiting streams was non-random so that 2 rural and 2 urban sites were sampled on the first day that collections were made each week, and 2 urban and 2 rural streams were visited on the second day. Streams of each type (urban and rural) were randomly chosen for sampling on day 1 or 2 at the start of the study, and streams were visited in the same order each week during the entire study. Collecting jars were filled about 1/3 full with 80% ethanol during the spring and autumn, and were filled about 1/2 with 80% ethanol in the summer to account for increased evaporation due to the increased temperatures. During each visit, the contents of each collecting jar were emptied into 500ml plastic bottles, and the collecting jars were refilled with 80% ethanol to the appropriate level and replaced on the traps.

Basic maintenance including 1) putting duct-tape over both sides of any small holes that formed in the mesh, 2) removing live spiders and webs from inside the trap and the collecting jars, and 3) tightening the support lines was done when visiting traps to collect samples. Minor damage, usually from storm flows or animals climbing on the traps, occurred more often at urban than rural sites. Minor damage such as small tears in the netting or a log being stuck in the baffle was not considered to have impacted the overall catch as long as the overall trap orientation was not compromised, and the data collected during these sample periods was not altered. The downstream sample at stream SAL collected during week 18 was lost when the trap was knocked down due to high stream flow during a storm event, and the data was standardized to account for the unequal sampling periods between traps at this site (see below).

Malaise trap samples were returned to the lab, sorted under magnification, and all caddisflies were removed. Samples were sorted in entirety, and specimens were removed, placed in 100% ethanol, and stored at -17ºC. All specimens were identified to the lowest practical taxonomic level with species level identifications most typical (see Appendix C for list of references used). A morphospecies designation was assigned to specimens that lacked taxonomic keys. A morphospecies is a synthetic designation for a group of specimens that share certain morphological features and are likely one unknown species. Identifications were checked against the Barcode of Life Data (BOLD) system database using DNA barcoding (see Appendix D for details). Individual samples from either side of the trap were sorted and identified individually, and community data from individual samples were aggregated during analysis (see below).

Table 2.2. Deployment dates and total days sampled for each week at each headwater stream.

		Wk1		Wk2		Wk6		Wk10		Wk14	
	Site	Deployed	Days	Deployed	Days	Deployed	Days	Deployed	Days	Deployed	Days
Rural	DRK	19-Mar	11	30-Mar	7	26-Apr	7	24-May	8	22-Jun	7
	PAT	15-Mar	16	31-Mar	7	27-Apr	7	25-May	8	23-Jun	7
	PTX	24-Mar	9	2-Apr	6	27-Apr	7	25-May	8	23-Jun	7
	SNC	25-Mar	5	30-Mar	7	26-Apr	7	24-May	8	22-Jun	7
Urban	GMT	23-Mar	7	30-Mar	7	26-Apr	8	24-May	8	22-Jun	7
	RBR	D: 27 / U: 23-Mar[a]	D: 4 U: 19[a]	31-Mar	7	27-Apr	7	26-May	7	23-Jun	7
	SAL	22-Mar	8	30-Mar	7	26-Apr	8	25-May	7	22-Jun	7
	SPD	16-Mar	15	31-Mar	7	27-Apr	7	26-May	7	23-Jun	7

		Wk18		Wk22		Wk26		Wk30		Wk34	
	Site	Deployed	Days	Deployed	Days	Deployed	Days	Deployed	Days	Deployed	Days
Rural	DRK	20-Jul	7	16-Aug	7	16-Aug	7	11-Oct	8	8-Nov	8
	PAT	21-Jul	7	16-Aug	8	16-Aug	6	13-Oct	7	10-Nov	7
	PTX	21-Jul	7	18-Aug	5	18-Aug	6	13-Oct	7	10-Nov	7
	SNC	20-Jul	7	16-Aug	8	16-Aug	7	11-Oct	8	8-Nov	8
Urban	GMT	20-Jul	7	16-Aug	7	16-Aug	7	11-Oct	8	8-Nov	8
	RBR	21-Jul	7	17-Aug	7	17-Aug	6	13-Oct	7	10-Nov	7
	SAL	20-Jul	7	16-Aug	7	16-Aug	7	11-Oct	8	8-Nov	8
	SPD	21-Jul	7	18-Aug	6	18-Aug	6	13-Oct	7	10-Nov	7

[a] D = Downstream and U = Upstream

Habitat assessments

Measures of habitat and physiochemical properties of each stream were done within a 40m reach centered at the Malaise trap location at the upstream and downstream sampling locations. Measures of substrate type, embeddedness, flow type, thalweg depth, habitat, and stream width were done at 11 transects across the stream channel spaced 4m apart within each 40m reach. A visual assessment was used to estimate the benthic substrate type(s) that comprised over 50% of the stream bottom. Substrates included silt, sand (<2mm and granular), gravel (2-10mm), pebble (1-6.4cm), cobble (6.4-25.6cm), boulder (>25cm), and bedrock. The stream bottom at each transect was considered embedded if over 50% of the benthic substrates were surrounded by fine sediments or sand with no interstitial spaces evident. A visual assessment was used to determine if riffle, run, or pool habitat (or combination of types) comprised greater than 50% of the flow types at each transect. The presence/absence of different habitat types included logs, woody debris, aquatic vegetation, root balls, debris dams, muck, leaf packs, backwater areas, and undercut banks were recorded for each transect. Stream depth in the thalweg and the wetted channel width were measured at each transect, and discharge was measured only at the downstream reach along a single transect using cross sectional area and stream flow measured with a Marsh-McBirney Flow-Mate model 2000 flow meter. Percent shading of the riparian canopy cover was measured at a single location within each sampling reach. A photograph was taken of the canopy from the middle of the stream reach at the Malaise trap. The program ImageJ (National Institutes of Health, Washington, DC) was used to determine the percent of the canopy that was open to the sky.

Water chemistry was assessed at the downstream reach of each headwater stream. Conductivity was measured using a YSI model 30 conductivity meter (Yellow Springs Instruments, Yellow Springs, Ohio) in the field on June 1 and 2, 2010. Water grab samples were taken on November 11, 2010 and analyzed for pH, chloride, sulfate, total nitrogen (TN), and total phosphorus (TP) by Ken Staver at the Wye Research and Education Center. Stream water temperature was monitored continuously for 1 year at the downstream reach using TidbiT v2 water temperature data loggers (Onset Computer Corporation, Bourne, MA). Data loggers were deployed so that logging began on June 25, 2010 at 000hrs. The June data logger deployment date was after Malaise traps were deployed, and as a result, direct comparisons of characteristics of the adult caddisfly assemblage with stream temperature were not possible. Temperature data was only used to describe the overall differences in water temperature between urban and rural headwaters. Temperature was recorded every 2 minutes. Data loggers were downloaded weekly until November 22/23, 2010, and after that, data loggers were downloaded on January 20, March 15, May 13, and July 8, 2011. The loggers were found outside of the stream on several occasions due to high flow events or vandalism. Data from the weeks affected by logger removal were removed from all 8 sites for analysis, and comparisons of temperature were done during periods of time when valid data was collected at all 8 sites. As a result, no temperature data was analyzed for December, 2010.

Analysis

Unless noted, caddisfly abundances were standardized based on the total deployment time of traps for the remainder of the analyses. Abundances were standardized to the number of caddisflies caught per 7 days for each individual “weekly” sampling period. Richness was not standardized based on sampling effort. In all cases, a headwater stream was considered a sample unit.

Sampling effort was assessed by comparing species rarefaction curves between streams. Species rarefaction by sample was calculated with Ecosim (v7.71, Acquired Intelligence Inc., Kesey-Bear, Jericho, VT) using unstandardized data for caddisfly abundance. The 10% rule proposed by Cain (1938) was used to determine adequacy of sampling. The 10% rule is an arbitrary level of increase in species accumulation per area sampled that indicates a minimal adequate amount of area was sampled. The minimum area occurs along the accumulation curve when an increase in 10% of the total species richness occurs along 10% of the total area sampled (Cain 1938). The rarefaction curves used in this analysis, however, were based on number of samples rather than area. The 10% rule was modified based on Zhao (2010) so an adequate amount of sampling occurred when a 10% increase in species richness occurred across 10% of the samples (rounded up to whole number) along the accumulation curve. Thus, sampling was considered adequate if the percent increase in taxa richness across the required number of samples along the rarefaction curve was less than 10% of the total species richness at the stream. In addition, the total abundance and richness across all 8 sites were compared between weeks to investigate seasonal patterns of the overall caddisfly catch during this study.

Comparisons of abundance, richness, time of peak abundance, and female:male sex ratio between rural and urban headwater streams were done with a Mann-Whitney U test (nonparametric) using the 4 streams as replicates for each treatment (R version 2.14.1; w*ilcox.test* protocol; *stats* package 2011). The few number of sample units made an assessment about the assumptions of parametric tests unreliable, and as a result, a more conservative non-parametric test was chosen. Comparisons of total richness and abundance used the summed abundance and total richness across all sample periods for each stream. Analysis of individual sample periods used the summed abundance and total richness across all 4 individual samples taken from both Malaise traps (2 traps with 2 samples from each trap) for each stream at that particular week. Comparisons of peak abundance were done for the entire caddisfly assemblage, *Dolophilodes distinctus* (Philopotamidae), *Chimarra aterrima* (Philopotamidae), *Cheumatopsyche analis*, *Glossosoma nigrior* (Glossosomatidae), and *Hydropsyche betteni* (Hydropsychidae). These taxa were chosen because they represented the most abundant taxa found consistently at both urban and rural streams. Comparisons of female:male sex ratio were done on the entire caddisfly assemblage, *D. distinctus*, *C. aterrima*, *C. analis*, and *H. betteni*. *G. nigrior* was excluded from this analysis because only 1 female was found at stream SPD.

Total caddisfly abundance and richness between up and downstream sample site locations were compared between urban and rural streams. Longitudinal patterns in abundance and richness may be due to longitudinal differences in the source assemblages along the stream (Smith and Lamp 2008) or due to dispersal patterns along the stream. The Malaise traps used in this study collected individuals from the up and downstream sides of the trap individually, but Macneale et al. (2004) reported that abundances of catches on different sides of a trap were a poor measure of migration direction. They stated that longitudinal differences in abundance of adults from a known (or suspected) source provided a better indication of movement direction (Macneale et al. 2004). The assemblage examined in this study is comprised of immigrants and residents that may have emerged from along the entire stream channel. Thus, a single source for the entire adult assemblage did not exist, and the factors determining longitudinal differences in abundance for the entire caddisfly assemblage (i.e., local source populations or dispersal patterns) are confounded. Percent richness at up and downstream sample site locations were calculated the number of taxa at a particular sample site location divided by the overall number of taxa caught at the stream. Up and downstream locations may share the same taxa, and as a result, percent richness can equal greater than 50% at both up and downstream locations. Richness is also determined by the same confounding factors that determine longitudinal differences in percent abundance. As a result, the longitudinal patterns of abundance and richness were examined without statistical analysis to only provide a description of the longitudinal patterns of adult caddisfly abundance and richness between rural and urban headwater streams.

Results

Habitat and physiochemical properties of headwater streams

Habitat was not markedly different between urban and rural headwater streams (Table 2.3). All streams had moderate slope (rural range 1% to 8%, urban range 1% to 5%), and were generally well shaded with intact riparian canopies. Benthic substrates were variable within urban and rural headwaters, but embeddedness was more common at urban than rural streams. Rural streams were all dominated by riffle habitat while urban streams were dominated by a mix of riffle, run, or pool habitat. Rural streams were generally shallower (average = 11.5cm) and narrower (average = 2.2m) than urban

Table 2.3. Physical characteristics of the headwater streams.

	Stream	Reach location	% slope	Canopy shading	Dominant substrate[a]	% Embedded	Dominant flow type (% occurred)	Mean depth (cm)	Mean width (m)	Number of habitat types
Rural	DRK	Down	1.5%	89.2%	P	0%	Riffle (100%)	6.6	2.05	5
		Up	2.0%	87.6%	C / Br	0%	Riffle (64%)	8.7	2.70	5
	PAT	Down	2.5%	94.9%	Sa	0%	Riffle (50%)	13.5	1.91	8
		Up	7.0%	88.9%	G / Br / Si	0%	Riffle (45%)	10.2	1.65	6
	PTX	Down	1.0%	79.7%	C / Bo / Si	0%	Riffle (55%)	18.0	2.38	5
		Up	8.0%	85.9%	Bo / C / G	0%	Riffle (64%)	13.1	1.49	6
	SNC	Down	1.0%	92.2%	P	0%	Riffle (91%)	12.4	3.50	7
		Up	4.0%	91.5%	G / Br / P / Bo	18%	Riffle (82%)	9.4	2.13	4
Urban	GMT	Down	1.5%	86.8%	Br / Sa	9%	Riffle (64%)	16.1	2.47	6
		Up	1.0%	76.0%	C	55%	Riffle (55%)	20.7	2.88	6
	RBR	Down	5.0%	87.6%	C	27%	Run (45%)	18.3	4.19	8
		Up	3.0%	89.4%	C / Br	27%	Run / Riffle (36%)	25.3	2.44	9
	SAL	Down	4.0%	85.8%	Bo	36%	Pool (55%)	19.1	4.07	6
		Up	2.0%	90.8%	Br / C / Bo	27%	Run (50%)	19.3	3.59	7
	SPD	Down	1.0%	83.1%	Sa / Bo	27%	Run (50%)	21.4	2.71	7
		Up	2.0%	86.0%	C	91%	Run (55%)	14.5	3.42	6

[a] For the dominant substrate types, P = Pebble, C = Cobble, Br = Bedrock, Bo = Boulder, Sa = Sand, Si = Silt, G = Gravel. Multiple substrate types were dominant if a single type made up less than 50% of the stream bottom

streams (average = 19.3cm depth and 3.22m width). The number of habitat types present within each stream reach varied between 4 and 8 for the rural streams and between 6 and 9 at the urban streams. The high number of habitat types indicated that habitats were generally diverse across rural and urban streams.

The chemical properties of the streams also varied between urban and rural headwaters (Table 2.4). Conductivity measured in the field was greater at urban (range of 271.2 to 565.0 μs) than rural (range of 48.0 to 158.8 μs) streams. Chloride concentrations were also greater at urban (range 46.3 to 161.3ppm) than rural (range 4.7 to 23.0ppm) streams. The pH was generally similar across all streams (7.32 to 7.73). Total nitrogen and TP varied within the rural streams (0.1 to 6.7ppm and 0.006 to 0.015ppm respectively), and TP was generally greater in the urban than rural streams. The higher TN values for the SNC and DRK streams were likely due to agricultural land in SNC's watershed and a golf course in DRK's watershed. Mean monthly water temperature for each stream type (rural and urban) was calculated from the individual

Table 2.4. Table of stream chemistry values from single grab samples taken at each headwater stream on November 11, 2010, and a field measurement for conductivity from June 1 and 2, 2010.

	Stream	Conductivity (μs)	pH	Cl (ppm)	SO4 (ppm)	TN (ppm)	TP (ppm)
Rural	DRK	112.6	7.32	16.9	0.8	4.1	0.007
	PAT	105.5	7.50	18.8	4.7	0.1	0.010
	PTX	48.0	7.46	4.7	0.4	2.3	0.006
	SNC	158.8	7.55	23.0	1.3	6.7	0.015
Urban	GMT	534.0	7.69	108.7	3.8	3.4	0.014
	RBR	271.2	7.58	46.3	4.5	3.5	0.020
	SAL	565.0	7.73	161.3	3.6	2.0	0.019
	SPD	440.8	7.56	103.7	6.8	3.2	0.021

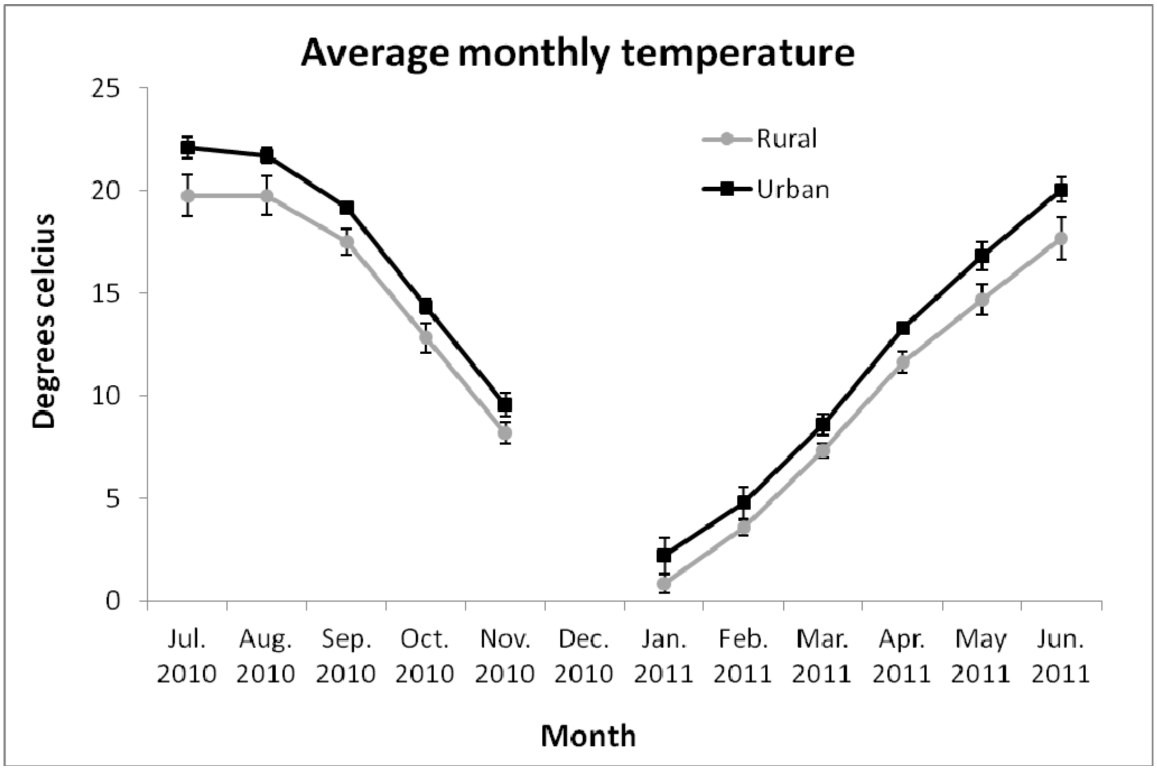


Fig. 2.3. Average monthly water temperature for urban and rural headwater streams. Error bars represent the standard deviation of individual monthly average values from the 4 means calculated for each type of stream. Data from June 2010 and July 2011 were excluded to demonstrate a yearly pattern. Data from part of November, 2010 through part of January 2011 was excluded due a lack of concordance in temperature data between streams. Outlier values were removed from the description as well.

mean monthly temperatures from the 4 urban and 4 rural headwater streams. Overall mean monthly temperature was generally higher at urban than rural streams, and variability was generally higher for rural than urban streams (Fig. 2.3).

Abundance and richness patterns at urban and rural streams

A total of 16,156 caddisflies from 50 different taxa (species, spp., or morphospecies) were caught during the 10 weeks (see chapter 3 for a list of taxa of adult caddisflies caught in this study). Caddisfly taxa caught belonged to 32 different genera and 18 different families. Groups of specimens belonging to the orders *Cheumatopsyche* (Hydropsychidae) and *Hydroptila* (Hydroptilidae) could not be identified to species and were left at *Cheumatopsyche* spp. and *Hydroptila* spp. respectively. Morphospecies designations were assigned to 1 species of *Ironoquia* (Limnephilidae) and 1 species of *Lepidostoma* (Lepidostomatidae).

The total number of individuals caught across all 8 sites was lowest during the beginning and end of the sampling extent of the study (Fig. 2.4a). The peak overall abundance across all 8 streams occurred during week 14 (Table 2.2). Total richness was also the lowest at the beginning and end of the sampling extent of the study (Fig. 2.4b). Peak richness across all 8 streams occurred during week 10 (Table 2.2). The overall pattern for richness across all 8 sites through time differed from the pattern for abundance. Weeks 10 and 14 had much higher abundances than the other weeks, and richness generally stayed high from week 10 to 26 (Table 2.2) (range of 26 to 30 taxa for each of those weeks).

Rarefaction curves generally reached an asymptote for all rural and urban streams based on the 10% rule proposed by Cain (1938) and modified by Zhao (2010) for species accumulation based on samples (Fig. 2.5). Total richness ranged from 33 to 38 species at the rural streams and from 7 to 23 taxa at the urban streams (Fig. 2.5). Total samples ranged from 36 to 38 at the urban streams and 28 to 37 at the urban streams. Samples without caddisflies were excluded from analysis and caused the differences in sample number betweens streams. The target percent increase in species richness per 10% of the samples ranged from 3.3% to 3.6% for the rural streams and 0.7% to 2.3% for urban streams (0.7% occurred for SPD). Based on the number of samples, percent increase in species richness was calculated for the estimated richness values between every 4th sample along the rarefaction curve (e.g., the percent increase was calculated between sample 1 and 4, 2 and 5, and so forth) except at SPD, which was calculated across every 3rd sample.

Percent increase in taxa richness fell below the 10% of total richness cutoff at all rural streams between 22 and 25 samples. GMT and SAL fell below the 10% cutoff at 34 and 29 samples respectively. RBR and SAL did not fall below the 10% cutoff based on total richness at the stream. The minimum increase in species richness along the rarefaction curve of 2.27% at RBR was close to the 2.1% cutoff. In addition, only 33 samples were collected at RBR, and the percent increase in taxa richness along the RBR rarefaction curve falls below 2.1% at week 24 if the percent increase in richness was calculated across every 3rd sample. The minimum percent increase in richness of 2.33% at SPD was not close to the 0.7% cutoff. The few number of taxa at this stream and large number of samples without caddisflies resulted in the low richness and low cutoff value. In addition, SPD had the lowest numerical increases in estimated richness during the last 10 samples of any stream (Fig. 2.5). Sampling was considered adequate at SPD based on the small numerical increases in estimated richness and the large number of samples without caddisflies.

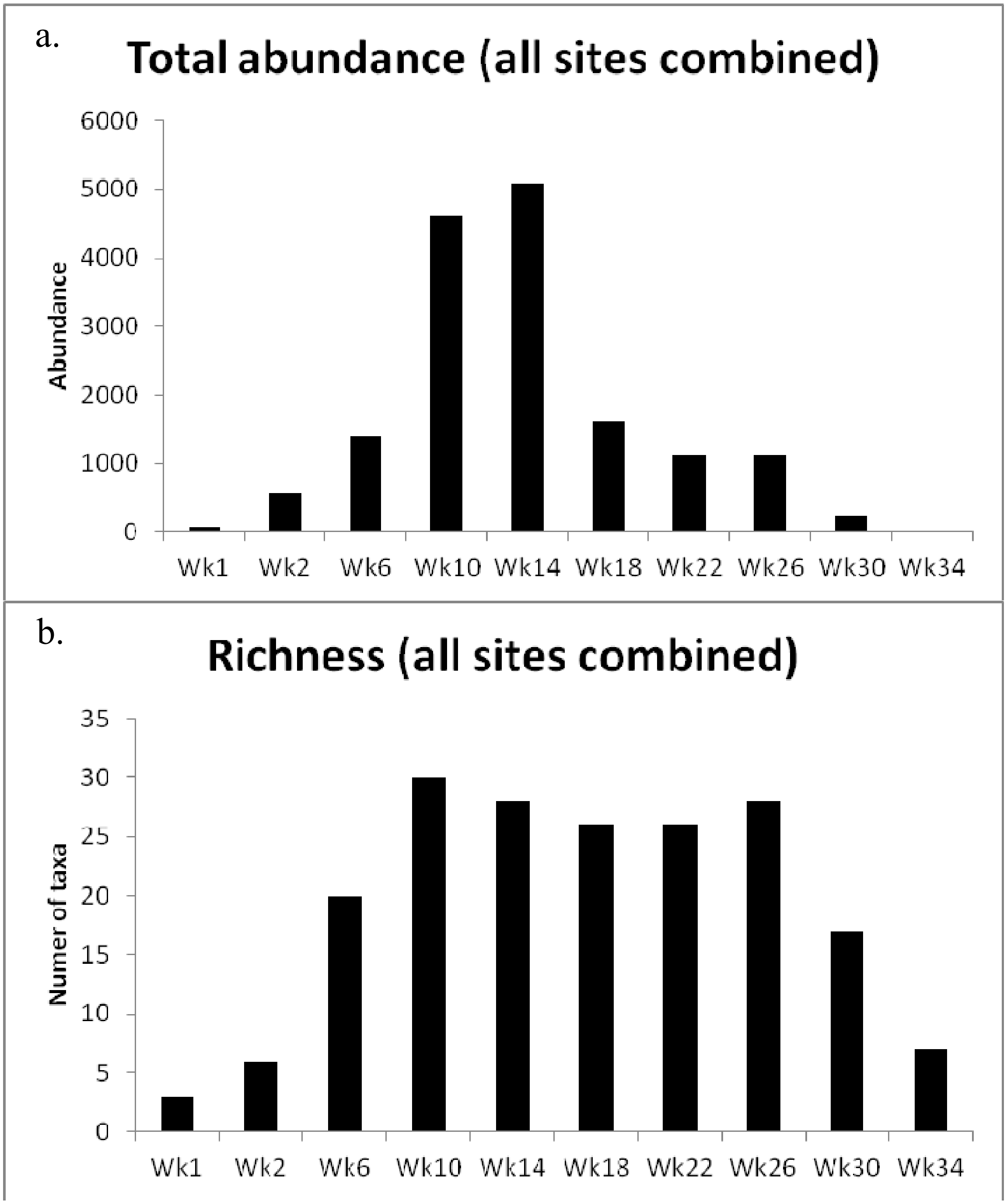


Fig. 2.4. a. Total abundance of caddisflies from all streams for all weeks sampled, and b. total richness of caddisflies from all streams for all weeks sampled. Sample dates are listed in table 2.2.

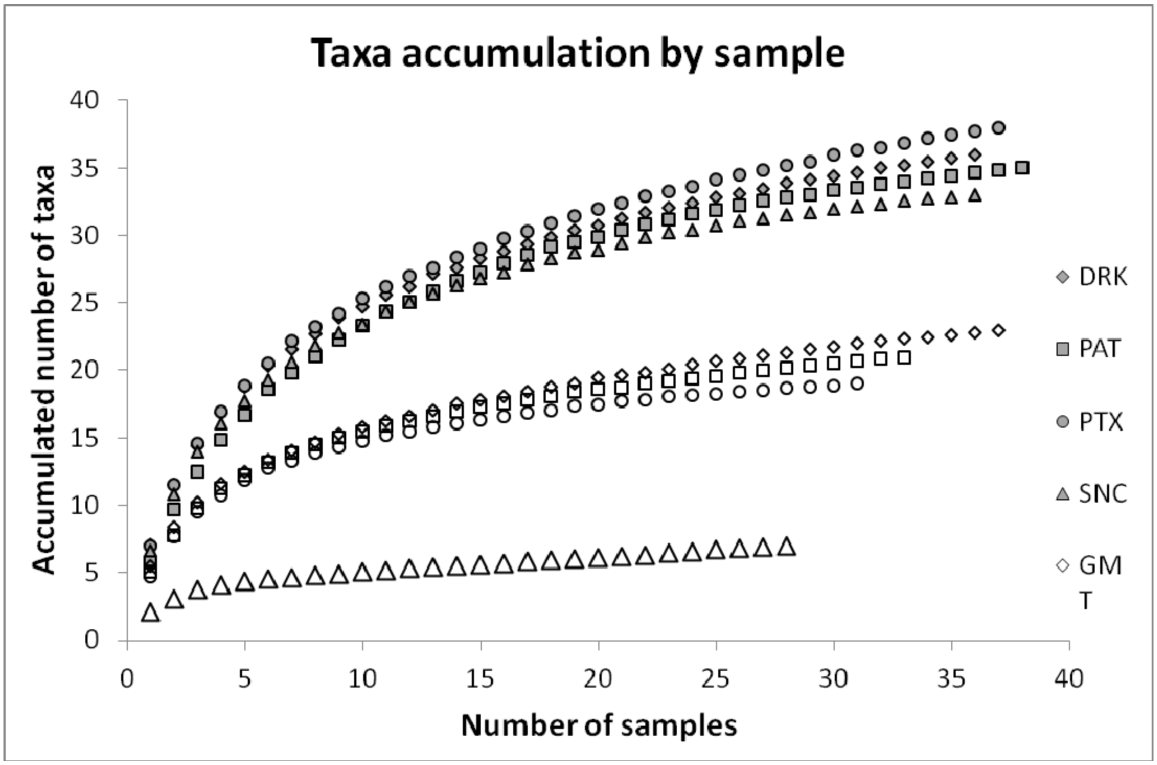


Fig. 2.5. Taxa rarefaction curves based on number of samples. Grey shaded symbols are the rural streams while the open symbols are the urban streams. The number of samples containing no caddisflies differed between streams and caused the total samples accumulated for each stream to differ. Rarefaction is based on total richness values of 33, 35, 36, and 38 species at SNC, PAT, DRK, and PTX respectively for the rural streams and 7, 19, 21, 23 species at SPD, SAL, RBR, and GMT respectively for the urban streams.

Total caddisfly abundance collected across all weeks for a stream was not significantly different between rural and urban headwaters (W = 11, *p* = 0.49, Fig. 2.6). Total standardized abundance per site ranged from 1,611.9 to 4,184.9 individuals/7d at the rural streams and 273 to 3,603.5 individuals/7d at the urban streams. Total caddisfly richness (unstandardized) collected across all weeks was significantly greater at rural than urban headwaters (W = 16, *p* = 0.03, Fig. 2.7). Total richness per stream ranged from 33 to 38 trichopteran taxa at the rural streams and 7 to 23 trichopteran taxa at the urban streams.

Abundance patterns for urban and rural streams followed a similar distribution through time (Fig. 2.8). The highest abundances were generally found in weeks 10 and 14, with the maximum individual abundance at rural streams occurring in week 14 and the maximum individual abundance at urban streams occurring in week 10 (Fig. 2.8). Comparisons of standardized abundance between urban and rural streams for each sampling week individually found that a statistically significant difference only occurred at week 34 when rural stream abundance was greater than urban stream abundance (W = 15.5, $p = 0.041$). Richness patterns through time at rural and urban streams both followed the same general pattern as the richness summed across all 8 streams (Fig. 2.4b) with taxa richness being high from week 6 through 26 and low during beginning and end of the study (Fig. 2.9). A significantly greater number of taxa were caught at rural than urban streams for weeks 10 (W = 16, $p = 0.029$), 14 (W = 16, $p = 0.028$), 18 (W = 16, $p = 0.028$), 22 (W = 15.5, $p = 0.042$), 26 (W = 16, $p = 0.029$), and 30 (W = 16, $p = 0.018$) (Fig. 2.9).

Peak abundance

Peak abundance for the entire caddisfly assemblage was generally later at the rural than urban streams (Table 2.5), though the difference was not statistically significant (W = 12, $p = 0.25$). The week of peak abundance differed significantly between urban and rural streams for only *D. distinctus* (W = 16, $p = 0.013$) (Table 2.5). The other taxa analyzed showed similar patterns of later peak abundances at rural than urban streams (Table 2.5), but no statistically significant differences were found. Total abundance at the week of peak abundance varied across all sites and within urban and rural streams (Table 2.5). In addition, the maximum number of *G. nigrior* at SPD was 1 individual, and peak abundance times should be interpreted with this information in mind.

Upstream/downstream comparison

The percent abundance of caddisflies sampled at up and downstream sample site locations varied between streams (Fig. 2.10a). Greater than 50% of the individuals were captured at the upstream location for 2 rural streams (PTX and SNC) and 1 urban stream (SPD). RBR had the greatest difference between the percent individuals caught at the upstream (9.4%) and downstream (90.6%) locations.

The percent richness of caddisflies sampled at up and downstream sample site locations were generally high at both locations for all streams (Fig. 2.10b) and indicated overlap in species composition occurred between up and downstream locations. The lowest percentage was found at the upstream location at RBR (57.1%). The downstream locations at SAL (100%) and RBR (95.2%) had the 2 highest percentages. No general differences between rural and urban streams were evident from the data.

Sex ratio

Female:male sex ratios based on the total abundance of each gender at a stream showed a general trend towards more females than males being caught above the stream channel across all streams for the entire caddisfly assemblage and each species analyzed (Table 2.6). A ratio > 1 indicates a bias towards a greater number of females than males, and this occurred at 7 streams for the entire caddisfly assemblage, 6 streams for *D.*

distinctus, 6 streams for *C. aterrima*, 7 streams for *C. analis*, and all 8 streams for *H. betteni*. No significant difference in female:male ratio was detected between urban and rural streams using a Mann Whitney U-test for the entire caddisfly assemblage or any of the species analyzed (Table 2.6).

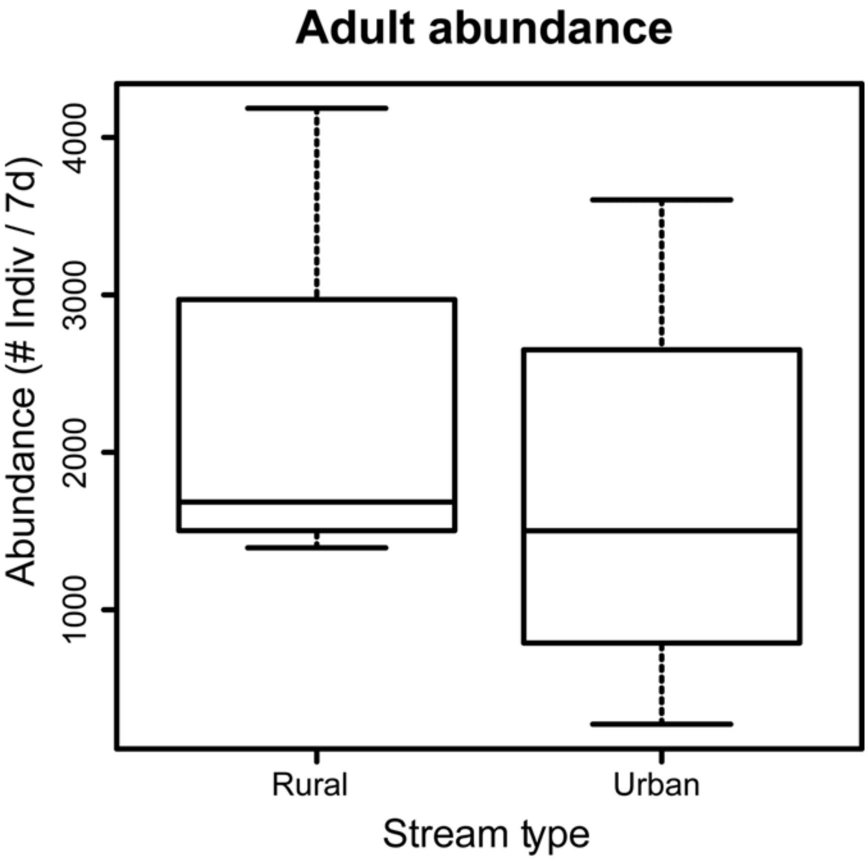


Fig. 2.6. Box and whisker plot of adult abundance values compared between rural and urban streams (W = 11, p = 0.49). Whiskers represent the minimum and maximum abundance values for each stream type.

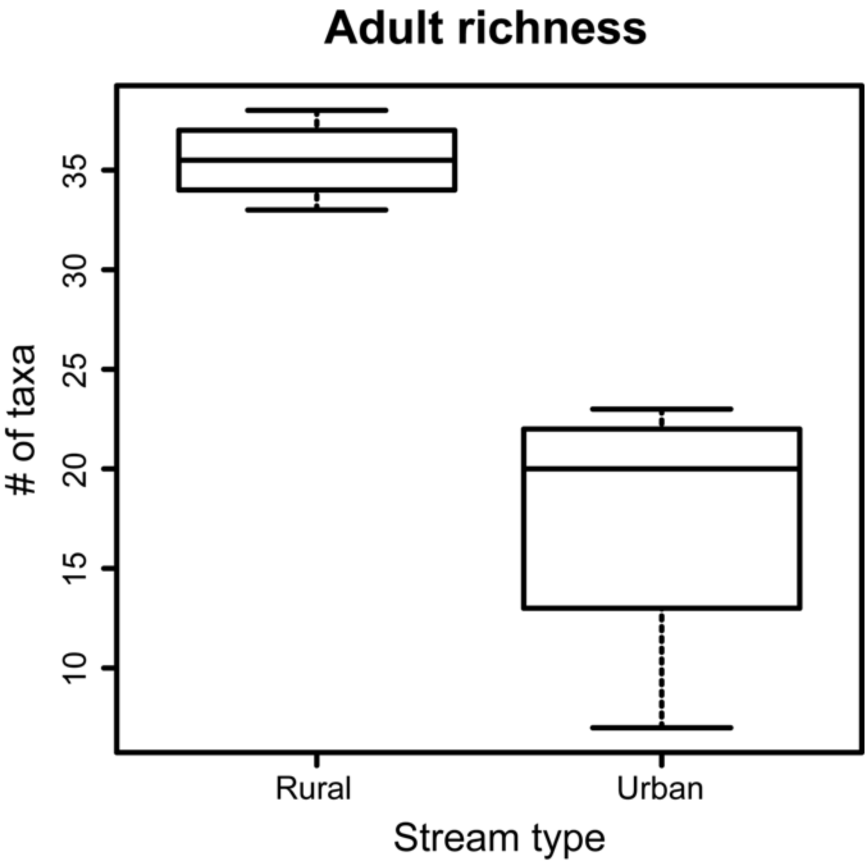


Fig. 2.7. Box and whisker plot of adult taxa richness values compared between rural and urban streams (W = 16, $p = 0.03$). Whiskers represent the minimum and maximum taxa richness values for each stream type.

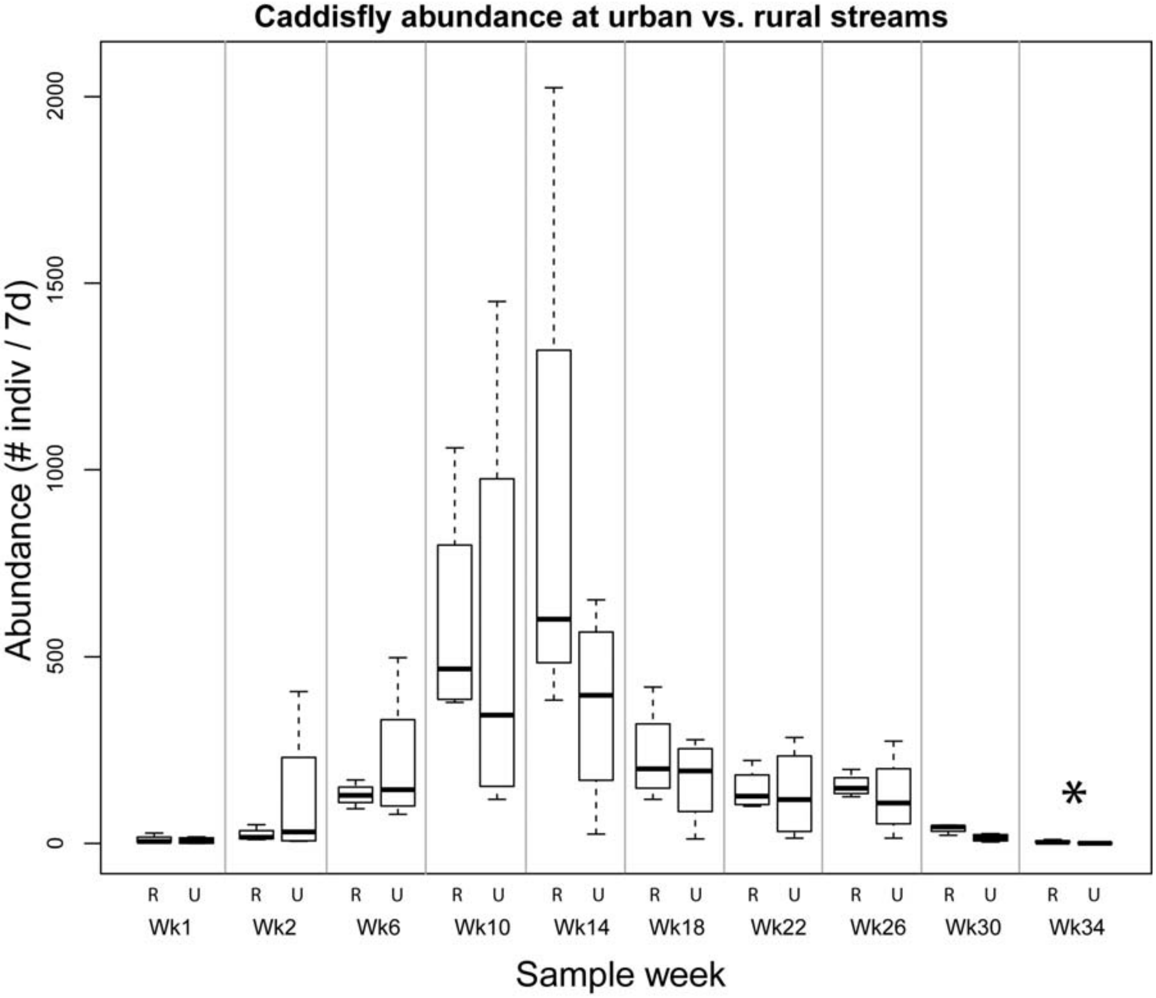


Fig. 2.8. Box and whisker plots of standardized adult abundances between urban and rural streams for each week. For each week, rural streams are represented by the box on the left (R) and urban streams represented by the box on the right (U). The * denotes a significant difference at *p* = 0.05 using a Mann-Whitney U test. Sample dates are listed in table 2.2.

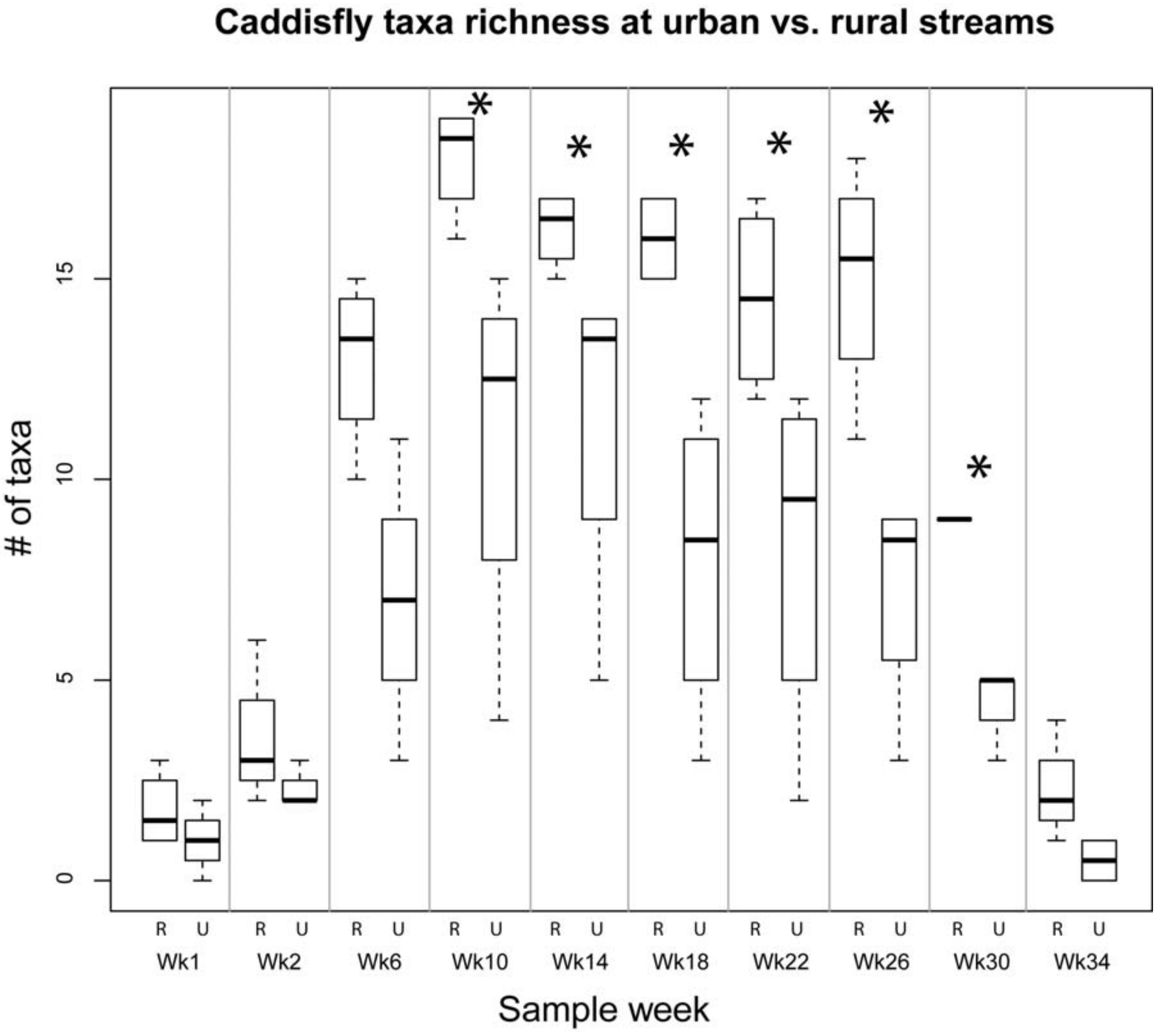


Fig. 2.9. Box and whisker plots of adult taxa richness between urban and rural streams for each week. For each week, rural streams are represented by the box on the left (R) and urban streams represented by the box on the right (U). The * denotes a significant difference at $p = 0.05$ using a Mann-Whitney U test. Sample dates are listed in table 2.2.

Table 2.5. Week of peak abundance for the entire caddisfly assemblage and 5 species shared by rural and urban streams for each stream. See Table 2.2 for deployment dates for each week.

		All Caddis		*D. distinctus*		*C. aterrima*		*C. analis*		*G. nigrior*		*H. betteni*	
	Site	Max ab.[a]	Week[b]	Max ab.[a]	Week[b]	Max ab.[a]	Week[b]	Max ab.[a]	Week[b]	Max ab.[a]	Week[b]	Max ab.[a]	Week[b]
Rural	DRK	617	14	388	14	17	6	5	6	11	14	14	18
	PAT	585	14	324	14	26	14	14	14	47	14	38	6
	PTX	2024	14	1492	14	4	18	1.75	10	31	14	16	14
	SNC	394.6	10	216	14	13	18	3	14	58	14	23	18
Urban	GMT	480	14	36.8	10	346	14	56.9	6	63	14	11.4	10
	RBR	1451	10	62	10	1062	10	344	2	63	2	37	10
	SAL	500	10	410	10	134	14	65.7	6	11	14	31.5	6
	SPD	118	10	3	10	7	6	62	10	1	2	19	6
U-test result[c]:		W = 12, $p = 0.25$		W = 16, $p = 0.013$		W = 11.5, $p = 0.37$		W = 13.5, $p = 0.13$		W = 12, $p = 0.18$		W = 13, $p = 0.18$	

[a] Max ab. is the abundance of the entire caddisfly assemblage or individual taxon at the week of peak abundance

[b] Week is the week that the peak abundance was observed

[c] The results of the Mann-Whitney U test comparing the week of peak abundance between rural and urban streams for the entire assemblage and for each species

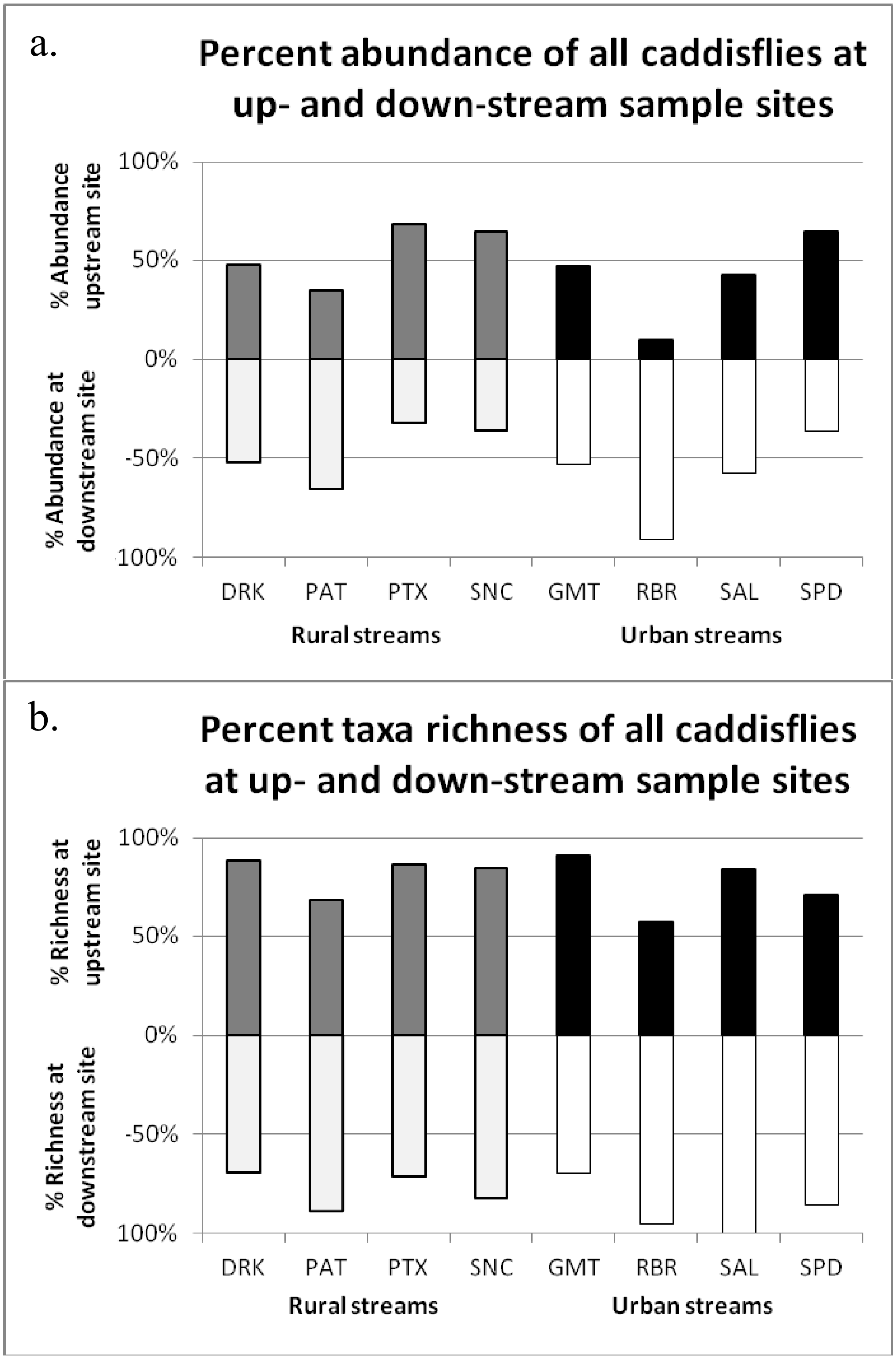


Fig. 2.10. Percent abundance (a, top) and richness (b, bottom) of the entire adult caddisfly assemblage found at the upstream and downstream sample site locations at each stream.

Table 2.6. Total abundance and female:male sex ratio for entire caddisfly assemblage and 4 species shared by rural and urban streams at each stream.

		All caddisflies		*D. distinctus*		*C. aterrima*		*C. analis*		*H. betteni*	
	Site	Total no.[a]	F:M[b]	Total no.[a]	F:M[b]	Total no.[a]	F:M[b]	Total no.[a]	F:M[b]	Total no.[a]	F:M[b]
Rural	DRK	1611.9	1.450	759.8	1.694	35.8	4.396	5.0	1.500	27.6	12.813
	PAT	1755.9	1.654	729.8	1.742	47.9	0.921	24.3	3.319	95.7	4.672
	PTX	4184.9	1.628	2425.2	2.129	10.4	2.467	3.9	1.238	54.0	2.014
	SNC	1393.5	1.585	543.5	1.114	25.6	1.181	7.8	0.590	60.5	9.298
Urban	GMT	1699.0	1.398	85.8	1.257	858.1	1.159	261.8	1.741	41.0	45.857
	RBR	3603.5	0.973	85.3	0.668	2114.8	0.796	892.8	1.291	99.5	3.975
	SAL	1304.6	1.185	657.0	0.693	198.3	2.104	226.5	2.445	58.5	4.087
	SPD	273.0	1.984	3.0	2.000	24.3	1.086	156.3	2.487	35.3	7.833
U-test result[c]:		W = 12, $p = 0.34$		W = 12, $p = 0.34$		W = 12, $p = 0.34$		W = 5, $p = 0.49$		W = 8, $p = 1.0$	

[a] Total no. is the total standardized abundance

[b] F:M is the ratio of female abundance to male abundance

[c] The result of the Mann-Witney U test comparing the female:male ratios between rural and urban streams for each species

Discussion

Caddisfly life stages interact with their environment at different spatial scales. As a result, mechanisms controlling population and community level processes likely act at the spatial scales important to each life stage. Alterations to in-stream habitat and the terrestrial landscape due to land use urbanization may alter the composition of the adult caddisfly assemblage (Paul and Meyer 2001, Fahrig 2007, chapter 1). The goal of this study was to describe the spatial and temporal differences in adult caddisfly abundance and richness between urban and rural headwater streams to determine the effect of land use urbanization on the adult caddisfly assemblage. Urban land use had a strong impact on richness, but less of an impact on spatial and temporal patterns of abundance and female:male sex ratios.

Community comparisons

Abundance generally did not differ between urban and rural streams, but taxa richness was generally greater at the rural than urban streams. The lower taxa richness found at urban streams was likely caused by reduced fitness of adult and larval caddisflies combined with dispersal constraints at the landscape scale. Decreased community richness of the larval insect assemblages living in streams is a common response to watershed urbanization (Allan and Flecker 1993, Paul and Meyer 2001, Walsh et al. 2005), and the composition of the adult assemblage is related to the composition of the assemblage emerging from streams (Banks et al. 2007). High percent embeddedness, conductivity, and instream temperatures indicated that in-stream habitat and water quality were poor in the urban headwaters. In addition, urban landscapes may have decreased fitness of the adult stage (chapter 1), which may have also contributed to decreased adult diversity at urban headwaters. Dispersal constraints may have limited immigration of adult individuals from nearby source populations in the urban landscape (chapter 1) and prevented rescue from local extirpation. Comparisons of the adult to the larval assemblages and a discussion of dispersal limitations are presented in chapter 3 of this dissertation. Regardless, the clear decrease in richness at the urban streams indicated that some aspect of urban headwater stream ecosystems and/or urbanized landscapes decreased diversity of adults but had little effect on abundance.

Increased productivity by the few caddisfly taxa remaining in urban streams may have resulted in similar abundances between urban and rural streams. High production by the larval assemblages supplying the adults to urban streams may have equaled or exceeded that of unimpacted streams (Alexander and Smock 2005). The most abundant taxa at each urban stream were *C. aterrima* (50.51% and 58.69% of all individuals at GMT and RBR respectively), *D. distinctus* (50.36% of all individuals at SAL), and *C. analis* (57.26% of all individuals at SPD), which are all filter feeders as larvae (Wiggins 2004, Morse and Holzenthal 2008). High levels of production are often found in communities dominated by filter feeders (Huryn and Wallace 2000). Locally high production resulting in high larval abundance of these species even in poor conditions of urban streams (Alexander and Smock 2005) may have supported the observed high abundances of adult populations at urban headwaters.

Peak abundance was generally earlier at urban than rural streams, but the patterns were only statistically significant for *D. distinctus*. Higher stream temperature or poorer food resources in urban than rural streams may have caused earlier emergence for caddisflies from the urban streams (Li et al. 2011, Kominoski et al. 2012). The temporal extent of the in-stream temperature data did not match entirely with the overall extent of malaise trap sampling, but in-stream water temperature was warmer in the urban than rural headwaters during the time water temperature was monitored. Adult caddisflies may have also accumulated for longer periods of time at rural than urban streams due to higher survival at or decreased emigration from rural streams (chapter 1). High survival and low emigration could delay the time of peak abundance from the time of peak emergence since individuals can persist longer in rural terrestrial environments. In contrast, low survival at or high emigration from urban streams may have caused adult abundance at a particular time to result solely from the emergence density that occurred at the same time without a lag in peak abundance. In-stream conditions that altered emergence times and terrestrial conditions that altered adult dispersal and survival may have caused the observed differences in peak abundance, but further research is needed to examine these potential mechanisms.

Assemblage wide patterns of peak abundance were related to the abundance patterns of the 2 most abundant taxa (*D. distinctus* and *C. aterrima*). *D. distinctus* was highly abundant at rural sites and had the same peak abundance times as the entire assemblage at 3 of the rural headwaters, and *C. aterrima* was highly abundant at the urban streams and had the same peak abundance times as the entire assemblage for 2 of the urban streams. Interspecific differences in the responses to altered aquatic and terrestrial habits or natural differences in life history processes by *D. distinctus* and *C. aterrima* substantially impacted the observed differences in overall peak abundance.

Upstream/downstream comparison

Longitudinal patterns of abundance and richness did not show a clear difference between rural and urban headwater streams. The causes for longitudinal patterns of percent abundance and richness were likely specific to individual streams. Species-specific differences in adult dispersal patterns, differences in the larval assemblage between streams, longitudinal differences in in-stream environment, and differences in the natural and anthropogenic features of the landscapes surrounding each stream may have caused the observed patterns (Paetzold and Tockner 2005, Wagner 2005a, Banks et al. 2007, Fahrig 2007). Greater larval taxa richness at downstream locations along the urban headwaters (Smith and Lamp 2008) may have caused the higher percent adult richness at the downstream site observed at 3 of the urban headwaters.

Sex ratio

No statistically significant difference between female:male sex ratios was found between urban and rural streams. Urbanization did not alter sex ratios of the entire adult caddisfly assemblage or the species examined in this study. Unique effects to males and females may have occurred in a way that abundance declines canceled each other out. For example, higher mortality by males may be offset by greater emigration rates by females. Decreased abundances at urban sites resulting from increased mortality and emigration, however, were not observed.

Adult behavioral traits could have led to the greater proportion of females caught over the stream at most headwaters. Other studies have observed a female bias in the adult caddisfly assemblage inhabiting the area above the stream channel (Kovats et al. 1996, Petersen et al. 1999). One hypothesis is that females migrate to the riparian zone and then back to the natal stream prior to oviposition, and males mate and migrate away from the stream without returning (Petersen et al. 1999). Thus, female bias results from sampling only above the stream channel. If this hypothesis is true, urbanization apparently did not alter the dispersal patterns and reproductive behavior of male and female caddisflies.

Sampling methods

The sampling methods employed in this study provided a robust representation of the adult caddisfly assemblage at urban and rural streams. Temporal patterns of total abundance and richness across all 8 streams indicated that sampling through time may be important for describing the entire caddisfly community. The low abundance of caddisflies sampled early and late during the study suggested that the majority of adult caddisfly individuals were present during the sampling extent employed in this study. Total richness was also low early and late during this study, which suggested that an extended sampling regime may be optimal for assessing overall assemblage richness. Rarefaction curves generally indicated that sampling was adequate based on the 10% rule, except at SPD. The periodic sampling through time from the spring to the fall provided a representative sample of the adult caddisfly assemblage at rural and urban streams, but additional sampling may be needed at urban streams with extremely low abundance.

Comparisons of abundance and richness between urban and rural streams may not require such an extensive sampling design. Sampling for a short period during peak abundance times may not sufficiently capture all taxa in the assemblage, but comparisons of taxa richness and abundance for individual weeks during the middle of the summer when peak abundance occurred produced the same results as for the overall community (Figs. 2.6, 2.7. 2.8, and 2.9). In fact, weekly measures of abundance and richness patterns at multiple weeks produced the same results as the comparisons of overall abundance and richness between urban and rural streams. Short-term Malaise trap samples may be sufficient to compare abundance and richness between urban and rural streams if assessing the overall species pool at the streams is not required.

Summary

Overall caddisfly abundance and abundance at individual (i.e. weekly) sampling periods generally did not differ between urban and rural streams, Urban streams, however, had fewer overall taxa of adult caddisflies than rural streams, and urban streams had fewer taxa of adult caddisflies during weeks 10 through 30 of this project (late May to mid October). Decreased community richness likely resulted from changes to in-stream and terrestrial habitat quality in urbanized landscapes. Differences in peak abundance were generally not statistically significant, but the observed differences in peak abundance between urban and rural streams may be biologically important. Sex ratios were not altered by urbanization for the species analyzed. The sampling methods employed by this study provided a thorough description of the adult caddisfly community at urban and rural streams, but this level of sampling may not be needed for coarse comparisons of abundance and richness between urban and rural streams.

Chapter 3: Constrained dispersal contributes to the loss of caddisfly (Trichoptera) taxa from headwater streams in urban landscapes

Abstract

Dispersal between habitats is important for population persistence and can determine community diversity of a habitat patch. Land use change for human use may increase fragmentation, decrease the permeability of matrix habitat, or create physical barriers to migration at the landscape scale. Land use change may also decrease the suitability of environmental conditions within the patch. I examined the importance of regional (dispersal mediated) and local (habitat mediated) processes resulting in decreased taxa richness of the larval caddisfly assemblage in urban headwater streams. The approach taken was to compare the adult to the larval caddisfly assemblage at 4 rural and 4 urban headwater streams. I hypothesized that urban headwaters had lower richness of adults and larvae than rural headwaters, which suggests that limited immigration to urban headwaters contributed to diversity loss. I also hypothesized that adult caddisfly taxa were found at urban streams where their larvae were absent, which suggests that poor in-stream environmental conditions contribute to diversity loss as well. Adult caddisflies were collected using Malaise traps, and larvae were collected with d-nets. Analysis of the assemblage was done using nonparametric and multivariate techniques, and examination of land use patterns at the landscape scale were done using GIS. Fewer taxa of adult and larval caddisflies were found at urban than rural headwaters, which indicated that dispersal constraints were acting regionally to limit colonization of urban headwaters. The number of immigrants to urban headwaters ranged from 3 to 14 taxa, which suggested that poor in-stream environmental conditions (locally) also prevented colonization and contributed to taxa loss. Caddisfly immigrants to urban streams were more male biased than the group of immigrants to rural streams and the entire adult assemblage at urban and rural streams. Male bias may limit colonization by immigrants and contribute to low diversity at urban headwaters. Non-urban land use surrounding the streams at .1 and .5km radii was greatest at urban streams with high levels of immigration. This land use pattern suggested that regional processes at small spatial scales may impact richness at urban headwaters. I concluded that regional and local processes were acting simultaneously in a hierarchical fashion to reduce larval diversity at urban headwater streams, and that regional processes are dependent on patterns of urban land use at the landscape scale. The implications of this work for stream conservation and restoration are also discussed.

Introduction

The movement of individuals across the landscape and the suitability of the environment within habitat patches are important factors determining the dynamics of populations and communities patchily distributed across a landscape (Ricklefs 1987, Roughgarden 1989, Stacey et al. 1997). Dispersal and habitat suitability interact to determine population growth, extinction, and colonization rates, which determine species presence/absence and overall metapopulation persistence (Roughgarden 1989, Ims and

Yoccoz 1997, Hanski 1998). Patterns of presence/absence for multiple populations determine the taxonomic composition of communities within individual habitat patches and for the entire metacommunity across all patches (Leibold et al. 2004). The processes controlling population and community dynamics related to dispersal and habitat suitability are defined by the spatial scales that they operate. Dispersal occurs between habitat patches at the landscape scale, and can be characterized as a regional process. In contrast, the suitability of habitat patches for populations and communities is based on processes that operate within the patch and are characterized as local processes. Population persistence and community diversity in single or multiple patches may depend predominantly on either a local or regional process in some instances (Mackay 1992), but local and regional processes typically function together to control patterns of presence/absence and diversity (Palmer et al. 1996, Stacey et al. 1997, Brown et al. 2011).

The dependence of population persistence and community diversity on both local and regional processes is the foundation for many theories in population and community ecology. Ecological concepts such as source-sink (Dias 1996) and metapopulation dynamics (Hanski 1998) describe the population level consequences for movement of individuals between habitat patches that vary in environmental conditions. Source-sink dynamics occur because local populations experiencing negative population growth require rescue through immigration from neighboring populations with positive population growth (Dias 1996). The size and quality of patches locally are important determinants of colonization by individuals migrating across the landscape (regionally) (Hanski 1998). The metacommunity concept (Leibold et al. 2004) is an example of a theoretical framework that describes how the interaction of local and regional processes can be scaled up to determine richness and composition of the entire community. Metacommunity theory is based on 4 descriptions of processes controlling community composition and richness that vary in the predominance of local processes related to habitat suitability within patches and regional processes dependent on patterns of dispersal across the landscape (Leibold et al. 2004).

The movement of individuals is a regional process resulting from an interaction between geographic characteristics of the landscape and species specific responses to environmental characteristics of patch and inter-patch habitats. Movement between habitats can occur over large or short distances, and may occur by active or passive dispersal (Bilton et al. 2001). The distance, timing, and behavior of dispersal activities are based on a complex interaction between species adaptive traits and the prevailing environmental conditions experienced by dispersing and non-dispersing stages (Bowler and Benton 2005, Jannot et al. 2007). Geographic location of patches (distance and arrangement), inter-patch habitat (i.e., the matrix), patch size, and patch quality partly control the ability of individuals to move between and colonize neighboring habitat patches (Stacey et al. 1997, Ricketts 2001, Fahrig 2003). Large inter-patch distances and impermeable matrix habitat generally lead to greater isolation of patches and decreased inter-patch dispersal (Ricketts 2001).

Local processes are those dependent on the biotic and abiotic characteristics of the environment that impact the fitness of individuals inhabiting the patch. Species interactions such as competition or predation can determine the suitability of a habitat patch (Roughgarden 1989, Menge 2000). Habitat quality may also be related to food availability, habitat needed for reproduction, or other components of the habitat needed for species fitness (Mackay 1992, Beck 1995).

Studies examining the impacts of human activities on natural populations have acknowledged the potential importance of movement between habitats for population persistence and the maintenance of diversity (Fahrig and Merriam 1985, Fagan 2002, Williams et al. 2005). Areas impacted by human activities tend to increase fragmentation, alter microclimates, and create anthropogenic structures that impede dispersal (McIntyre 2000, Pickett et al. 2001, Fagen 2002, Elmore and Kaushal 2008). Factors impacting dispersal, however, are often ignored when examining the impact of human activities on species with perceived high levels of dispersal. For example, flight capable stream insects are not perceived to face significant dispersal constraints in urban areas, and as a result, regional processes are sometimes ignored when determining what structures communities in an urban landscape (Palmer et al. 1997, chapter 1).

The impacts of urban land use on the movement of the adult stage of stream insects through the terrestrial landscape may partly structure communities in urban streams (Urban et al. 2006); yet, empirical studies involving adults have received relatively little attention in urban stream ecology. Stream insect life cycles generally include an adult stage that lives outside the stream and a larval stage that lives in the stream. The adult stage is more mobile but shorter lived than the larval stage. The impacts of watershed urbanization on the fitness of larval stages are well known (Paul and Meyer 2001). Human activities in the watershed alter hydrologic, geomorphic, and chemical properties of the stream, which decreases the suitability of in-stream habitat for aquatic larvae (Walsh et al. 2005). The close association of the larval stage with the aquatic environment makes it the logical choice for studies focused on understanding and assessing the impairment caused by land use urbanization (Resh et al. 1995, Karr 1999, Huryn and Wallace 2000, Bonada et al. 2006). The information presented in chapter 1, however, suggests that human activities in urban areas may decrease survival and/or dispersal of adult stream insects, and these impacts may partly determine the richness and composition of larval insect communities in urban streams (Urban et al. 2006).

Studies of adult stream insect dispersal have mostly focused on determining the spatial preference for flight direction. A preference for upstream movement exists for many species, but not all, and the importance of movement upstream for repopulating upstream reaches is unresolved (Anholt 1995). High abundance above the stream channel suggests that dispersal along the stream channel occurs more frequently than through upland areas (Sode and Wiberg-Larsen 1993). Direct empirical evidence of preferential movement through the stream corridor is lacking, however, and work by Macneale et al. (2005) has shown that movement can occur between reaches through upland areas. Adult stream insects show a preference for movement into certain types of natural habitats (Petersen et al. 1999, Petersen et al. 2004), but a direct assessment of movement through urban areas is lacking (except see Purcell et al. 2002).

The unpredictability and low quality of the aquatic environment in urban streams (Paul and Meyer 2001) may lead to local extinctions and high turnover of larval populations, and a lack of adults immigrating to urban streams could limit population persistence by limiting population rescue (Palmer et al. 1996). Population rescue may be required following pulsed disturbances occurring over short temporal scales or following the remediation of long term (press) disturbances. Asynchronous population abundances through time due to dispersal constraints may limit mixing of reproductive adults between neighboring streams and decrease reproductive output (Calabrese and Fagan 2004). Isolated populations in urban streams may also suffer from a lack of gene flow (Alexander et al. 2011), which could also contribute to local extirpations.

This study determined the level of immigration to urban streams and the importance of regional (dispersal mediated) versus local (habitat mediated) processes for determining taxonomic composition of larval caddisfly assemblages in urban headwater streams. I hypothesized that urban landscapes limit the species of adult caddisflies migrating to urban streams and this lack of immigration (i.e., a regional process) contributes to low diversity of larval assemblages in urban headwaters. I compared the adult and larval trichopteran assemblages at urban versus rural headwater streams to determine levels of immigration to and colonization of urban headwaters. Longitudinal patterns of the abundance of immigrants and the gender of immigrants were also compared between urban and rural streams to further investigate the impact of urbanization on regional processes controlling assemblage composition.

Methods

General approach

The general approach used in this study to determine the level of immigration to urban streams and the importance of regional versus local processes for controlling the composition of the larval caddisfly assemblage was to compare richness and composition of adult to larval assemblages at urban and rural headwater streams. For this study, the term "local processes" refers to any factor that may prevent colonization such as a lack of oviposition habitat or mortality to the egg or larval stages. The framework used for analysis was based on 2 assumptions: 1) adult flight is the primary means of immigration by caddisflies in this study, and 2) larval richness is lower at urban than rural headwater streams. While downstream drift of larvae can occur over long distances, the headwaters sampled have no upstream reaches to supply drifting larval immigrants. In addition, swimming or crawling upstream are not considered legitimate methods for long-distance dispersal by caddisfly larvae (Jackson et al. 1999). The immobility of caddisfly larvae supports the first assumption that the main sources of immigrants to each headwater stream are flight capable adults. The second assumption is supported by numerous empirical studies that have repeatedly found low larval taxa richness in urban streams (see reviews by Paul and Meyer 2001, Walsh et al. 2005) including a study by Smith and Lamp (2008) that found lower taxa richness in urban than rural headwaters using 3 of the urban headwater streams included in this study.

Concordance of assemblage composition between local larval and adult assemblage depends on levels of immigration by adult caddisflies (Fig. 3.1). Constraints on immigration imposed by the landscape would make the local larval assemblage the primary supplier of taxa to the local adult assemblage. The main-stem that each headwater flows into is connected to each headwater at the confluence and is a likely source of at least a few taxa of immigrants poorly adapted to and unable to colonize headwater environments. Thus, complete isolation of headwaters is unlikely, and local in-stream habitat at each headwater naturally filters out a few species from the adult assemblage. Unconstrained immigration from the regional species pool to an urban headwater would add taxa to the local adult assemblage beyond those originating from the local larval assemblage or immigrating from the main-stem (Fig. 3.1a) (Heino et al.

2003b). When immigration is unconstrained, the composition and richness of the adult assemblage differ from the urban larval assemblage and are similar to the adult assemblage at unimpacted headwater streams (Fig. 3.1a). Constrained immigration from the regional species pool to an urban headwater would not add taxa to the local adult assemblage beyond those originating from the local larval assemblage or immigrating from the main-stem (Fig. 3.1b). When immigration is constrained, the composition and richness of the adult assemblage are similar the urban larval assemblage and differ from the adult assemblage at unimpacted headwater streams (Fig. 3.1b). By utilizing the *a priori* assumption of lower larval richness in urban than rural headwaters, comparing adult richness between urban and rural headwaters can indicate if immigration is occurring freely (equal richness) or is constrained (lower richness at urban streams) (Fig. 3.1).

Comparing the composition of immigrant and resident groups of trichopteran taxa between urban and rural streams can indicate how local and regional processes are impacting specific groups of taxa. For this analysis, all taxa found at each stream were divided into 2 categories representing their immigration status. The immigrant group at a stream consisted of all taxa that were 1) present as adults at the stream and 2) absent as larvae from the stream. The resident group at a stream consisted of all taxa that were 1) present as adults at the stream and 2) present as larvae at the stream. Taxa found as adults and larvae at a stream were considered residents even though immigration may occur to locations where the larvae are present. Comparing the composition of immigrant and resident groups can indicate if the presence/absence of taxa is based on dispersal constraints (a regional process) or in-stream habitat constraints (a local process) at urban and rural headwaters.

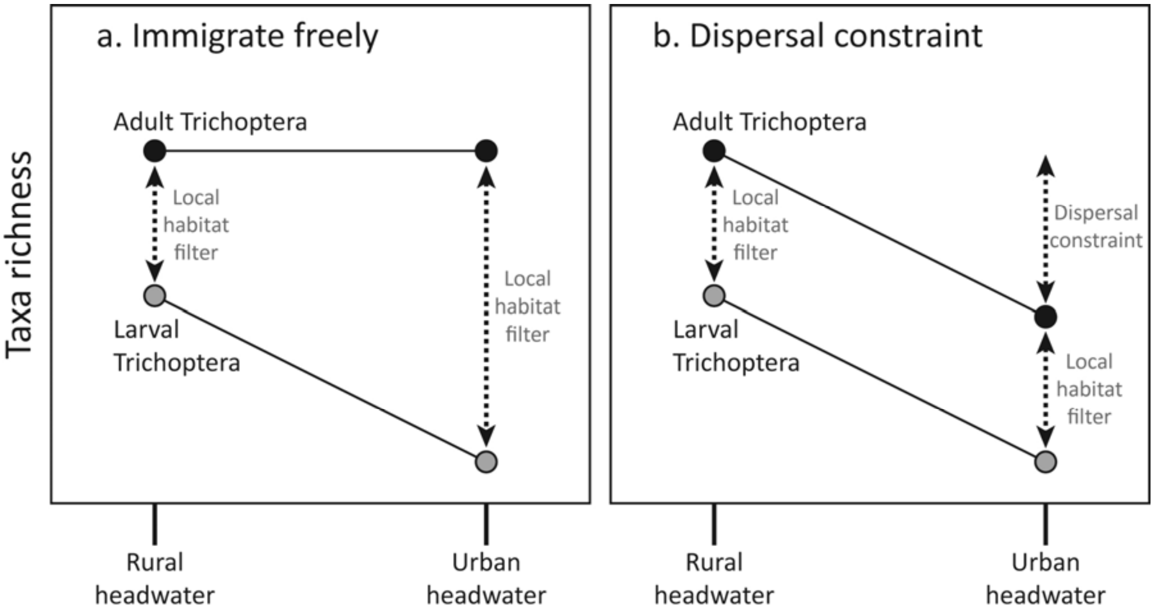


Fig. 3.1. Diagram explaining the use of adult species richness for determining if local or regional processes are structuring larval communities in urban headwaters. The framework is based on the *a priori* assumption that larval richness is lower in urban than rural headwaters. In box a, dispersal occurs without constraint, and local adult richness at urban headwaters is dependent on the regional species pool. In box b, dispersal is constrained, and adult richness is dependent primarily on local larval richness and as a result, is lower at urban than rural headwaters.

Methods described in chapter 2

The collections of adult caddisflies from the 4 rural and 4 urban headwater streams used for analysis in chapter 2 were also used for analysis in this chapter. Methods for site selection, habitat assessments, adult collections, and adult identifications were the same as described in chapter 2. Some taxa of adults were reclassified to a different taxonomic level to ensure consistency with the taxonomy of the larval assemblage. Taxonomic reclassification was required for comparing the composition of the adult and larval assemblages. Details of this are described below.

Larval field collections

Trichopteran larvae were collected from all 8 headwater streams in spring (April and May), summer (August), and autumn (November) 2010. Individuals were collected using a 25cm wide d-frame net at each Malaise trap location. Sampling was done within the same 40m reach with the Malaise trap at the center where measures of stream habitat were performed (chapter 2). Ten d-net samples were taken from all habitats within the 40m reach in the proportion that each habitat existed in the reach. A total of 20 d-net samples were taken from each stream for each season (60 samples total per stream). All 10 samples collected from a reach were combined in the field and preserved with 100% ethanol. D-net samples were returned to the lab, sorted under magnification, and all caddisfly larvae were removed.

Larval specimens were identified to the lowest practical taxonomic level with species identifications desirable (see Appendix C for list of references). Several groups lacked sufficient taxonomic data for species identifications and were identified to genus. Those groups were *Cheumatopsyche* spp., *Hydroptila* spp., *Lepidostoma* spp., *Pycnopsyche* spp., and *Polycentropus* spp. Species of adult caddisflies collected in chapter 2 belonging to these genera were also reclassified to this taxonomic level (see below).

Adult versus larval comparisons

Adult caddisflies identified in chapter 2 were reassigned to the same taxonomic level used for larval identifications for all comparisons of larval and adult assemblage richness and composition. Species or morphospecies of adults identified in chapter 2 belonging to the 5 genera listed above were reassigned to their genus level designations. All comparisons of larval and adult abundance and richness between urban and rural streams were done using the nonparametric Mann Whitney U-test with 4 replicates for each stream type (i.e., treatment) (R version 2.14.1; *wilcox.test* protocol; *stats* package 2011).

Analysis of assemblage composition of immigrant and resident groups

Analysis of the assemblage composition of immigrant and resident groups of caddisflies at urban and rural streams was done using a correspondence analysis (CA). A detrended correspondence analysis (DCA) was performed on log+1 transformed abundance data to determine the length of the gradient of the community data. The results indicated the data were unimodal (axis 1 gradient = 4.049), and a CA was appropriate (Lepš and Šmilauer 2003). The CA was performed on log+1 transformed abundance data using the type of assemblage (resident urban group, immigrant urban group, resident rural group, and immigrant rural group) as a categorical explanatory variable (i.e., environmental variable), which was passively displayed on the resulting ordination. The distance in ordination space between the centroids corresponding to these groups represents a general measure of dissimilarity between the groups. The samples representing the immigrant and resident groups from a single stream were not independent. As a result, a constrained analysis to determine if the type of assemblage explained a statistically significant portion of the variation in the community data was not performed. A CA was chosen over an NMDS to allow for species data to be presented in the ordination biplot. All multivariate analyses were done using CANOCO for Windows (version 4.5; Biometris—Plant Research International, Wageningen, The Netherlands).

Comparisons of abundance at up and downstream locations and of gender ratios between urban and rural headwaters were done for the immigrant taxa groups found at each stream. As stated in chapter 2, differences in abundance of adults between up and downstream sides of a trap are poor predictors of flight direction of adult stream insects (Macneale et al. 2004). Dispersal direction can be determined for the immigrant group since, by definition, their larvae are absent from the focal stream; and as a result, the adults must have originated from external source populations. In addition, the position of headwater streams at the ends of the stream network eliminates downstream movement by adults as a possible direction for immigration. Thus, longitudinal patterns of abundance can indicate if adult stream insects are moving upstream through the stream corridor from the mouth of the stream or dispersing through upland habitats (Macneale et al. 2004). Dispersal occurring in an upstream direction from flight through the stream corridor would result in a greater abundance of immigrants at the downstream location since flying adults enter the channel at the mouth of the stream. Dispersal through upland areas would result in no difference in abundance between the up and downstream sample site locations since flying adults enter the channel along the entire stream margin. The percent abundance of adults in the immigrant group at each stream was compared graphically, but no statistical test was performed.

A female bias was observed in chapter 2 for the entire caddisfly assemblage at urban and rural headwater streams, and as stated, the greater percent of females above the stream may be based on different migration patterns and reproductive behaviors of adult females and males (Petersen et al. 1999). Female abundance is important for recruitment, and any change in gender ratios to the immigrant group may indicate another mechanism leading to taxa loss. As a result, the percentage of males and females in the immigrant group at each stream were compared graphically.

Land use analysis

Percent urban, agricultural, and rural land use was calculated for 3 radii of different distances around each Malaise trap sampling site for each stream. Land use was calculated for radii at 0.1, 0.5, and 1km around the 2 sampling sites on each headwater. Overlapping areas were merged into a single area so the land use in the overlap was not counted twice. As a result, actual area covered by each pair of radii at a stream differed depending on the distance between sampling locations (i.e., sample sites far away had less overlap than those close together). Land use data used was the 2010 Maryland Department of Planning land use / land cover data (http://www.mdp.state.md.us/OurWork/landUseDownload.shtml).

Results

Abundance and richness of the larval trichopteran assemblage

A total of 2,472 larval caddisflies were sampled from all 8 headwater streams representing 26 different taxa. Larval caddisflies sampled belonged to 25 different genera and 14 different families. All larval caddisfly taxa were found in the adult assemblage across all 8 streams. Taxonomic reclassification of the adult caddisfly data from chapter 2 for consistency with the larval data set resulted in a total of 39 taxa of adults from all 8 headwater streams. The reclassification resulted in collapsing 16 taxa of adults into 5 taxa for a net loss of 11 taxa from the community data set used in chapter 2 (2 taxa into *Cheumatopsyche* spp.; 3 taxa into *Hydroptila* spp.; 5 taxa into *Lepidostoma* spp.; 3 taxa into *Pycnopsyche* spp.; 3 taxa into and *Polycentropus* spp.).

Abundance of larval caddisflies was not significantly different between urban and rural headwater streams (W = 14, *p* = 0.11, Fig 3.2). Abundances ranged from 91 to 671 specimens at the rural streams and from 33 to 282 specimens at the urban streams (Fig. 3.2). Richness of the larval caddisfly assemblage was significantly greater at rural than urban streams (W = 16, *p* = 0.028, Fig. 3.3). Richness ranged from 14 to 22 taxa at the rural headwaters and from 3 to 9 taxa at the urban headwaters. The assumption of the framework described in Fig. 3.1 that larval richness was lower at urban than rural headwater was supported.

Abundance and richness of the adult trichopteran assemblage

The adult caddisfly assemblages (based on taxonomic reclassifications) at the rural headwaters had significantly more taxa than the assemblages at the urban headwaters (W = 16, $p = 0.028$, Fig. 3.4). Taxa richness values ranged from 27 to 29 at the rural headwater and from 6 to 20 at the urban headwaters. Comparison of adult taxa richness between urban and rural streams using species level taxonomy (chapter 2) showed the same pattern of a significantly greater number of taxa at the rural than urban headwaters (Fig. 2.6). As stated in chapter 2, the abundance of the adult assemblage did not differ significantly between rural and urban headwaters (Fig. 2.5).

Comparison of the composition of adult and larval trichopteran assemblages

None of the sites contained all the trichopteran taxa collected throughout all of the sampling (i.e., the regional species pool) (Figure 3.5, with taxa information listed in Table 3.1). As expected from the patterns of larval taxa richness discussed above (Fig. 3.3), the number of taxa in the resident groups were lower at urban than rural streams. Immigrant taxa (i.e., adults present and larvae absent at a stream) were found at each stream (Fig. 3.5). The number of taxa in the immigrant group varied between 8 and 12 taxa at rural streams and between 3 and 14 taxa at the urban streams. The immigrant groups had 42% to 107% more taxa than the resident group at rural streams and 100% to 467% more taxa than the resident group at the urban streams (Table 3.2). In addition, the immigrant group abundances ranged from 49 to 306 at the rural streams and from 57 to 812 at the urban streams (Table 3.2).

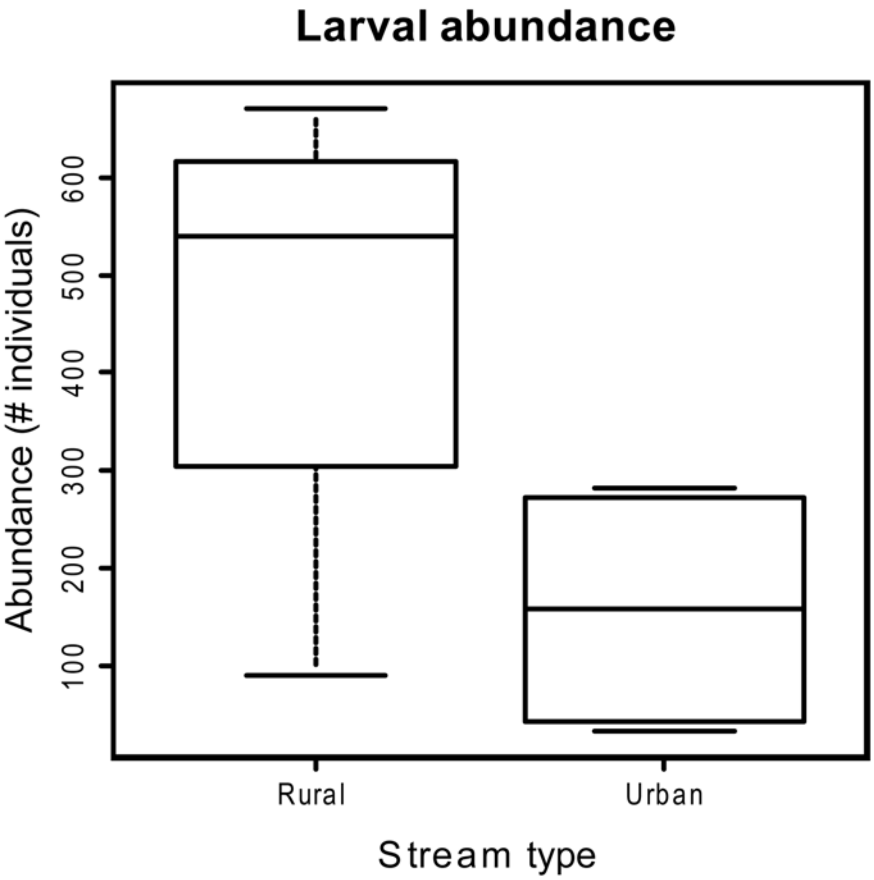


Fig. 3.2. Box and whisker plot of larval caddisfly abundance compared between rural and urban streams (W = 14, *p* = 0.11). Whiskers represent the minimum and maximum abundance values for each stream type.

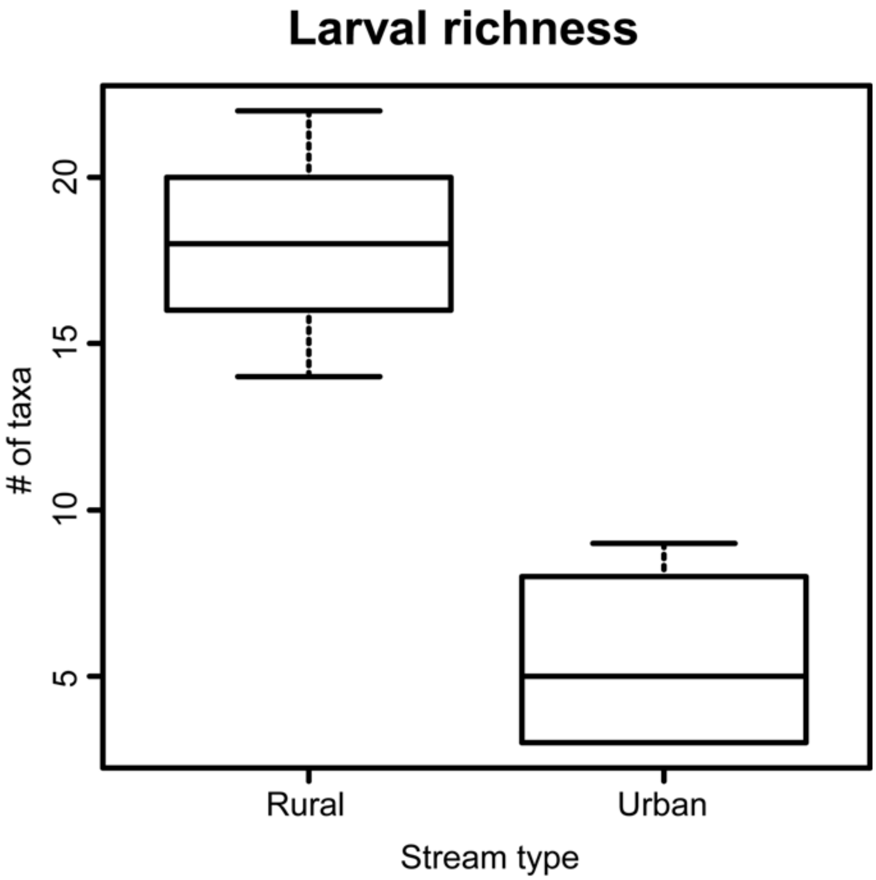


Fig. 3.3. Box and whisker plot of larval caddisfly taxa richness compared between rural and urban streams (W = 16, *p* = 0.028). Whiskers represent the minimum and maximum richness values for each stream type.

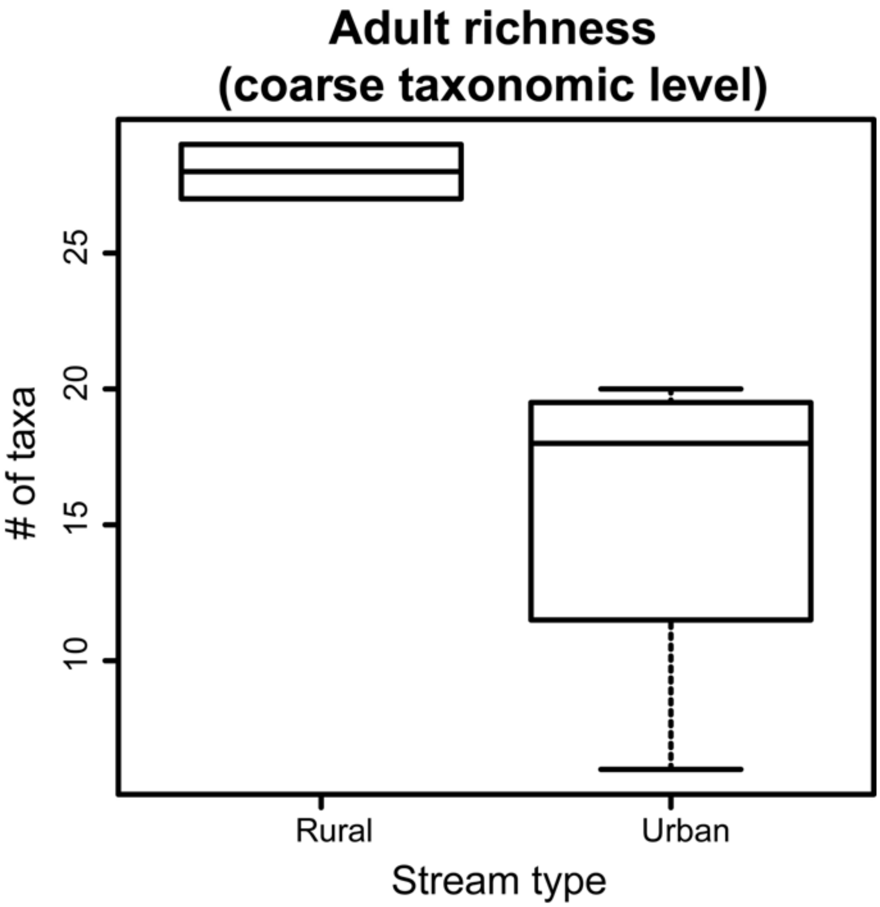


Fig. 3.4. Box and whisker plot of adult taxa richness compared between rural and urban streams (W = 16, *p* = 0.028). Richness was calculated from the taxonomic level used in larval samples. Whiskers represent the minimum and maximum richness values for each stream type.

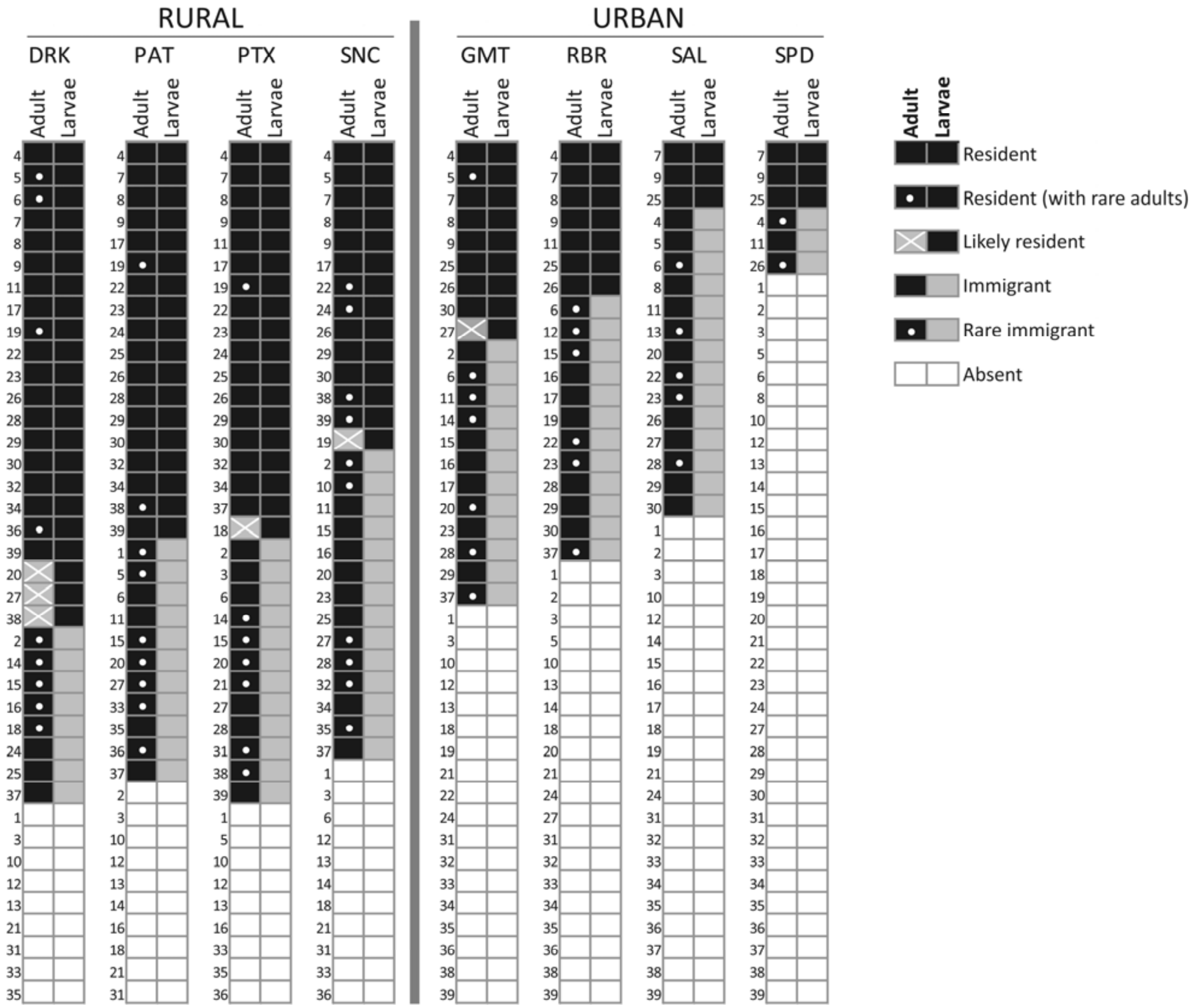
(Fig. 3.5 - caption)

Fig. 3.5. Chart of adult and larval caddisfly taxon presence / absence at each headwater stream. Each pair of columns represents a headwater stream. For each pair of columns, the taxa of adults are represented by the left column and the taxa of larvae are represented by the right column. Black boxes indicate the taxon is present, and grey and white boxes indicate that the taxon is absent. Numbers next to the column represent an individual taxon listed in Table 3.1. Likely residents refer to situations where the larva was collected but the adult was not. These taxa were assumed to reside at the stream since adults are needed for larval colonization, and the adults were present but likely not sampled. Rare immigrants represent immigrant taxa with a total unstandardized adult abundance ≤ 3 individuals. The total length of the column represents the regional taxa pool of caddisflies based on sampling for this study (39 taxa).

(Table 3.1 - caption)

Table 3.1. List of taxon identifications for Fig. 3.5, and a summary of presence/absence of adults and larvae at the 4 urban headwaters.

(Fig. 3.5 - illustration)



RURAL

DRK			PAT			PTX			SNC		
	Adult	Larvae		Adult	Larvae		Adult	Larvae		Adult	Larvae
4	■	■	4	■	■	4	■	■	4	■	■
5	◙	■	7	■	■	7	■	■	5	■	■
6	◙	■	8	■	■	8	■	■	7	■	■
7	■	■	9	■	■	9	■	■	8	■	■
8	■	■	17	■	■	11	■	■	9	■	■
9	■	■	19	◙	■	17	■	■	17	■	■
11	■	■	22	■	■	19	◙	■	22	◙	■
17	■	■	23	■	■	22	■	■	24	◙	■
19	◙	■	24	■	■	23	■	■	26	■	■
22	■	■	25	■	■	24	■	■	29	■	■
23	■	■	26	■	■	25	■	■	30	■	■
26	■	■	28	■	■	26	■	■	38	◙	■
28	■	■	29	■	■	29	■	■	39	◙	■
29	■	■	30	■	■	30	■	■	19	☒	■
30	■	■	32	■	■	32	■	■	2	◙	▨
32	■	■	34	■	■	34	■	■	10	◙	▨
34	■	■	38	◙	■	37	■	■	11	■	▨
36	◙	■	39	■	■	18	☒	■	15	■	▨
39	■	■	1	◙	▨	2	■	▨	16	■	▨
20	☒	■	5	◙	▨	3	■	▨	20	■	▨
27	☒	■	6	■	▨	6	■	▨	23	■	▨
38	☒	■	11	■	▨	14	◙	▨	25	■	▨
2	◙	▨	15	◙	▨	15	◙	▨	27	◙	▨
14	◙	▨	20	◙	▨	20	◙	▨	28	◙	▨
15	◙	▨	27	◙	▨	21	◙	▨	32	◙	▨
16	◙	▨	33	◙	▨	27	■	▨	34	■	▨
18	◙	▨	35	■	▨	28	■	▨	35	◙	▨
24	■	▨	36	◙	▨	31	◙	▨	37	■	▨
25	■	▨	37	■	▨	38	◙	▨	1	☐	☐
37	■	▨	2	☐	☐	39	■	▨	3	☐	☐
1	☐	☐	3	☐	☐	1	☐	☐	6	☐	☐
3	☐	☐	10	☐	☐	5	☐	☐	12	☐	☐
10	☐	☐	12	☐	☐	10	☐	☐	13	☐	☐
12	☐	☐	13	☐	☐	12	☐	☐	14	☐	☐
13	☐	☐	14	☐	☐	13	☐	☐	18	☐	☐
21	☐	☐	16	☐	☐	16	☐	☐	21	☐	☐
31	☐	☐	18	☐	☐	33	☐	☐	31	☐	☐
33	☐	☐	21	☐	☐	35	☐	☐	33	☐	☐
35	☐	☐	31	☐	☐	36	☐	☐	36	☐	☐

URBAN

GMT			RBR			SAL			SPD		
	Adult	Larvae		Adult	Larvae		Adult	Larvae		Adult	Larvae
4	■	■	4	■	■	7	■	■	7	■	■
5	◙	■	7	■	■	9	■	■	9	■	■
7	■	■	8	■	■	25	■	■	25	■	■
8	■	■	9	■	■	4	■	▨	4	◙	▨
9	■	■	11	■	■	5	■	▨	11	■	▨
25	■	■	25	■	■	6	◙	▨	26	◙	▨
26	■	■	26	■	■	8	■	▨	1	☐	☐
30	■	■	6	◙	▨	11	■	▨	2	☐	☐
27	☒	■	12	◙	▨	13	◙	▨	3	☐	☐
2	■	▨	15	◙	▨	20	■	▨	5	☐	☐
6	◙	▨	16	■	▨	22	◙	▨	6	☐	☐
11	◙	▨	17	■	▨	23	◙	▨	8	☐	☐
14	◙	▨	19	■	▨	26	■	▨	10	☐	☐
15	■	▨	22	◙	▨	27	■	▨	12	☐	☐
16	■	▨	23	◙	▨	28	◙	▨	13	☐	☐
17	■	▨	28	■	▨	29	■	▨	14	☐	☐
20	◙	▨	29	■	▨	30	■	▨	15	☐	☐
23	■	▨	30	■	▨	1	☐	☐	16	☐	☐
28	◙	▨	37	◙	▨	2	☐	☐	17	☐	☐
29	■	▨	1	☐	☐	3	☐	☐	18	☐	☐
37	◙	▨	2	☐	☐	10	☐	☐	19	☐	☐
1	☐	☐	3	☐	☐	12	☐	☐	20	☐	☐
3	☐	☐	5	☐	☐	14	☐	☐	21	☐	☐
10	☐	☐	10	☐	☐	15	☐	☐	22	☐	☐
12	☐	☐	13	☐	☐	16	☐	☐	23	☐	☐
13	☐	☐	14	☐	☐	17	☐	☐	24	☐	☐
18	☐	☐	18	☐	☐	18	☐	☐	27	☐	☐
19	☐	☐	20	☐	☐	19	☐	☐	28	☐	☐
21	☐	☐	21	☐	☐	21	☐	☐	29	☐	☐
22	☐	☐	24	☐	☐	24	☐	☐	30	☐	☐
24	☐	☐	27	☐	☐	31	☐	☐	31	☐	☐
31	☐	☐	31	☐	☐	32	☐	☐	32	☐	☐
32	☐	☐	32	☐	☐	33	☐	☐	33	☐	☐
33	☐	☐	33	☐	☐	34	☐	☐	34	☐	☐
34	☐	☐	34	☐	☐	35	☐	☐	35	☐	☐
35	☐	☐	35	☐	☐	36	☐	☐	36	☐	☐
36	☐	☐	36	☐	☐	37	☐	☐	37	☐	☐
38	☐	☐	38	☐	☐	38	☐	☐	38	☐	☐
39	☐	☐	39	☐	☐	39	☐	☐	39	☐	☐

Adult	**Larvae**	
■	■	Resident
◙	■	Resident (with rare adults)
☒	■	Likely resident
■	▨	Immigrant
◙	▨	Rare immigrant
☐	☐	Absent

(Table 3.1 - illustration)

Tx#[a]	Taxon	Res[b]	Imm[c]	Abs[d]	FFG[e]
1	Brachycentridae:*Micrasema wataga* MS[e]	0	0	4	SH/CG
2	Dipseudopsidae:*Phylocentropus lucidus*	0	1	3	CF
3	Glossosomatidae:*Agapetus walkerii*	0	0	4	SC
4	Glossosomatidae:*Glossosoma nigrior*	2	2	0	SC
5	Hydropsychidae:*Ceratopsyche bronta*	1	1	2	CF
6	Hydropsychidae:*Ceratopsyche sparna*	0	3	1	CF
7	Hydropsychidae:*Cheumatopsyche* spp.	4	0	0	CF
8	Hydropsychidae:*Diplectrona modesta* gr.[f]	2	1	1	CF
9	Hydropsychidae:*Hydropsyche betteni*	4	0	0	CF
10	Hydropsychidae:*Hydropsyche dicantha*	0	0	4	CF
11	Hydroptilidae:*Hydroptila* spp.	1	3	0	PH
12	Hydroptilidae:*Leucotrichia pictipes* MS[e]	0	1	3	CG
13	Hydroptilidae:*Orthotrichia cristata*	0	1	3	PH
14	Leptoceridae:*Mystacides sepulchralis*	0	1	3	CG
15	Leptoceridae:*Oecetis persimilis*	0	2	2	PR
16	Leptoceridae:*Trianodes ignites*	0	2	2	SH
17	Lepidostomatidae:*Lepidostoma* spp.	0	2	2	SH
18	Limnephilidae:*Frenesia missa/difficilis*	0	0	4	SH
19	Limnephilidae:*Hydatophylax argus*	0	1	3	SH
20	Limnephilidae:*Ironoquia* unknown MS[e]	0	1	3	SH
21	Limnephilidae:*Limnephilus submonilifer*	0	0	4	SH
22	Limnephilidae:*Pycnopsyche* spp.	0	2	2	SH
23	Molannidae:*Molanna blenda*	0	3	1	SC/CG/PR
24	Odontoceridae:*Psilotreta frontalis*	0	0	4	SC
25	Philopotamidae:*Chimarra aterrima*	4	0	0	CF
26	Philopotamidae:*Dolophilodes distinctus*	2	2	0	CF
27	Philopotamidae:*Wormaldia moestra*	1	1	2	CF
28	Phryganeidae:*Ptilostomis ocellifera*	0	3	1	SH/PR**
29	Polycentropidae:*Polycentropus* spp.	0	3	1	PR/CF/SH
30	Psychomyiidae:*Lype diversa*	1	2	1	SC*
31	Psychomyiidae:*Pyschomyia flavida*	0	0	4	GC/SC**
32	Rhyacophilidae:*Rhyacophila carolina*	0	0	4	PR
33	Rhyacophilidae:*Rhyacophila fuscula* MS[e]	0	0	4	PR
34	Rhyacophilidae:*Rhyacophila invaria*	0	0	4	PR
35	Rhyacophilidae:*Rhyacophila torva* MS[e]	0	0	4	PR
36	Sericostamatidae:*Agarodes griseus*	0	0	4	SH/CG
37	Uenoidae:*Neophylax concinnus*	0	2	2	SC
38	Uenoidae:*Neophylax mitchelli*	0	0	4	SC
39	Uenoidae:*Neophylax oligius*	0	0	4	SC

[a] Tx# references the taxon listed in the table to the numbers listed in Fig. 3.5

[b] Res. represents the number of urban streams at which the taxon was present as larvae and an adult. Taxa with this adult and larval presence/absence pattern were considered part of the resident group in Fig. 3.5

[c] Imm. represents the number of urban streams at which the taxon was present as an adult but absent as a larvae. Taxa with this adult and larval presence/absence pattern were considered part of the immigrant group in Fig. 3.5

[d] Abs. represents the number of urban streams at which the larvae and adults for the taxon were absent from the stream (see Fig. 3.5)

[e] FFG represents the primary functional feeding group(s) listed for the genus that each taxon belonged to from Morse and Holzenthal (2008). * indicates that a species level FFG designation was provided. ** indicates that only facultative FFG designations were listed. FFG abbreviations are CF: collector-filterer, SC: scraper, PR: predator, SH: shredder, PH: piercer-herbivore, and CG: collector-gatherer

[e] MS indicates a morphospecies resembling the species designation preceding “MS” in the listed taxon name. “Unknown” precedes MS if the morphospecies did not resemble a particular species found in the taxonomic keys available

[f] DNA barcoding results from chapter 2 indicated that *Diplectrona modesta* is not monospecific (unpublished data), and gr. indicates this taxon is potentially comprised of multiple cryptic species

Across all 8 streams, 6 taxa of larvae were found at streams where their adult taxa were not sampled (Fig. 3.5). These taxa were considered likely residents since adults are required for larval colonization, and as a result, these taxa were considered part of the resident group for all analyses. Rare adult taxa (total unstandardized adult abundance ≤ 3 individuals, determined arbitrarily) often represented the majority of immigrants at all rural and urban headwaters (Fig. 3.5). Rare adult taxa made up 62.5%, 63.6%, 50.0%, and 38.5% of the immigrant taxa at DRK, PAT, PTX, and SNC (the rural headwaters) respectively, and rare adult taxa made up 50%, 50%, 35.7%, and 66.7% of the immigrant taxa at GMT, RBR, SAL, and SPD (the urban headwaters) respectively (Fig. 3.5).

Patterns of presence/absence for adults and larvae for each taxon of caddisfly often differed among the 4 urban headwaters (Fig. 3.5, Table 3.1). Patterns of larval and adult presence/absence are described based on the classification of taxa at each stream as either part of the immigrant or resident groups (see methods above). Individual taxa may be part of one group at some urban streams and part of another group at the others, and patterns of adult and larval presence/absence can provide information about site specific differences in the processes determining colonization at urban headwaters. Of the 39 caddisfly taxa included in this study, 14 were absent from all 4 urban headwater streams. Of the remaining 25 caddisfly taxa present at 1 or more urban streams, 3 were part of the resident group at all 4 urban headwaters, and 7 were part of the resident group at 3 or fewer urban headwaters (Fig. 3.5, Table 3.1). Of the 7 caddisfly taxa that were part of the resident group at 3 or fewer urban headwater, 3 taxa belonged to only the immigrant and resident groups across all 4 urban headwaters (i.e., they were never absent), and 4 caddisfly taxa were part of the resident and immigrant groups and absent across all 4 urban headwaters. Never was a taxon of caddisfly part of the resident group at 1-3 urban headwaters and absent from all the rest.

The ordination biplot resulting from the CA displays the composition of immigrant and resident groups for rural and urban headwaters (Fig. 3.6). Axes 1 and 2 displayed in Fig. 3.6 represented 25.4% and 15.7% of the variance in the assemblage data respectively (total variance = 41.1%). While no statistical test was performed to determine if taxonomic groupings explained a significant amount of the variance in the community data, visual assessments of the location of the centroids representing the type of assemblage can provide information about differences in community composition. However, axis 1 (correlation coefficient = 0.930) was more correlated with groupings assigned to each type of assemblage (i.e., the explanatory variable) than axis 2 (correlation coefficient = .687). The variance explained and correlation to the type of assemblage suggested that axis 1 best described differences between the immigrant and resident assemblages at rural and urban streams. All four types of assemblages separated from each other along axis 1, and the centroids for the urban resident group and the rural immigrant group were the furthest from each other along axis 1. The centroid for the urban immigrant group fell between the centroids for the rural resident and rural immigrant groups, and the centroid for the rural resident group fell between the urban immigrant and urban resident centroids along axis 1. The urban resident group was defined by the presence of *Cheumatopsyche* spp., *Hydropsyche betteni*, and *Chimarra aterrima*. The rural immigrant community was defined by the presence of multiple species of *Rhyacophila* and *Micrasema wataga* MS.

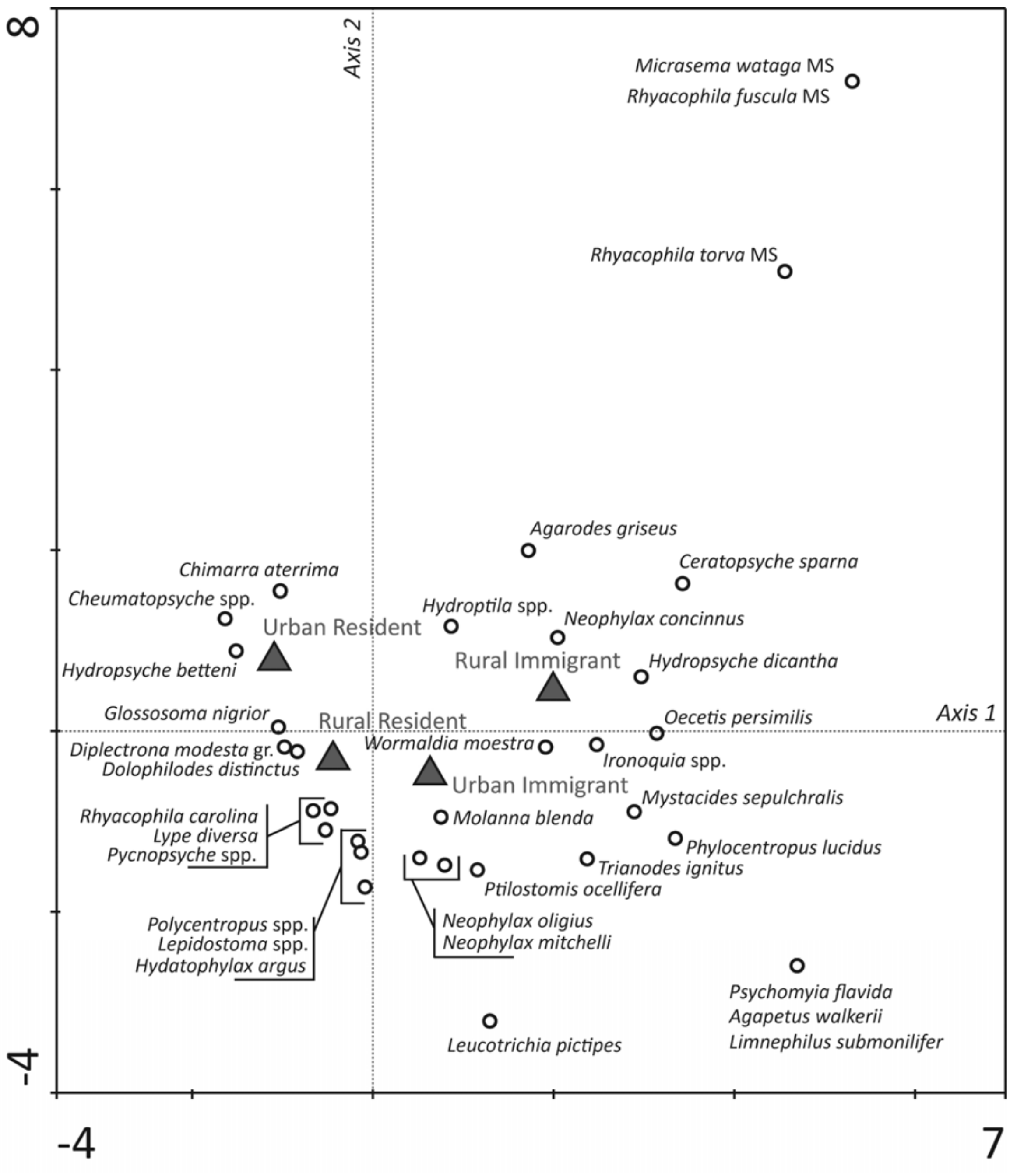


Fig. 3.6. Ordination bi-plot for the CA of adult caddisfly data with centroids representing the resident and immigrant groups for rural and urban streams passively overlaid on the bi-plot. CA is an indirect gradient analysis that does not allow a statistical test to determine if taxonomic groups explained a significant portion of the variance in the community data.

Radial land use analysis

The percent urban land use was lower at each spatial scale for the rural than urban streams except for the low amount of urban land use at SAL in the 0.1km radius (Table 3.2). SAL had the lowest amount of urban land use surrounding the sample sites of all 4 urban streams for all spatial scales analyzed (Table 3.2). SPD had the highest urban land use at 0.1km and GMT had the highest urban land use at 0.5 and 1km. Urban land use was generally not in close proximity to the rural streams, and riparian areas were generally forested (Fig. 3.7). The urban land near the upstream sample site location at DRK is mostly a golf course. The small amount of forested land use in the radii for the 4 urban streams was generally found in the riparian areas (Fig. 3.7), but the extent and location of the forested riparian areas differed among urban streams. While not formally measured as part of the analysis, the diagrams of land use around the sampling locations show that agricultural land use was more common around the rural than urban streams.

Upstream/downstream comparison of immigrants

The percent of immigrants found at the downstream and upstream locations varied for both urban and rural headwater streams (Fig. 3.8). The percentage at the downstream locations was over 50% for 2 of the rural streams and 3 of the urban streams, and the percentage at the downstream site for SNC was close to 50% at 48.7%. The most immigrants at a downstream location were found at RBR (94.1% of immigrants) and the lowest percentage of immigrants at the downstream location was 35.56% at GMT.

Table 3.2. Number of taxa belonging to the immigrant and resident groups at each stream.

	Stream	Immigrant taxa	Resident taxa	% Increase in taxa[a]	Immigrant abundance[b]	% Urban[c] (0.1km)	(0.5km)	(1km)
Rural	DRK	8	19	42.1%	72.5	3%	16%	23%
	PAT	11	18	61.1%	79	0%	4%	14%
	PTX	12	17	70.6%	49	0%	0%	0%
	SNC	14	13	107.7%	306	0%	8%	14%
Urban	GMT	12	8	150.0%	79	58%	72%	72%
	RBR	12	7	171.4%	134	58%	66%	68%
	SAL	14	3	466.7%	812	3%	32%	50%
	SPD	3	3	100.0%	57	71%	54%	57%

[a] Percent increase represents the overall percent increase in total taxa to the resident taxa when the immigrant taxa are added

[b] Immigrant abundance is the standardized abundance values for the immigrants to each site (see chapter 2 for description of standardization techniques)

[c] Percent urban land use represents the percent of land use that is commercial, residential, or industrial that occurred within each radius around the sample sites

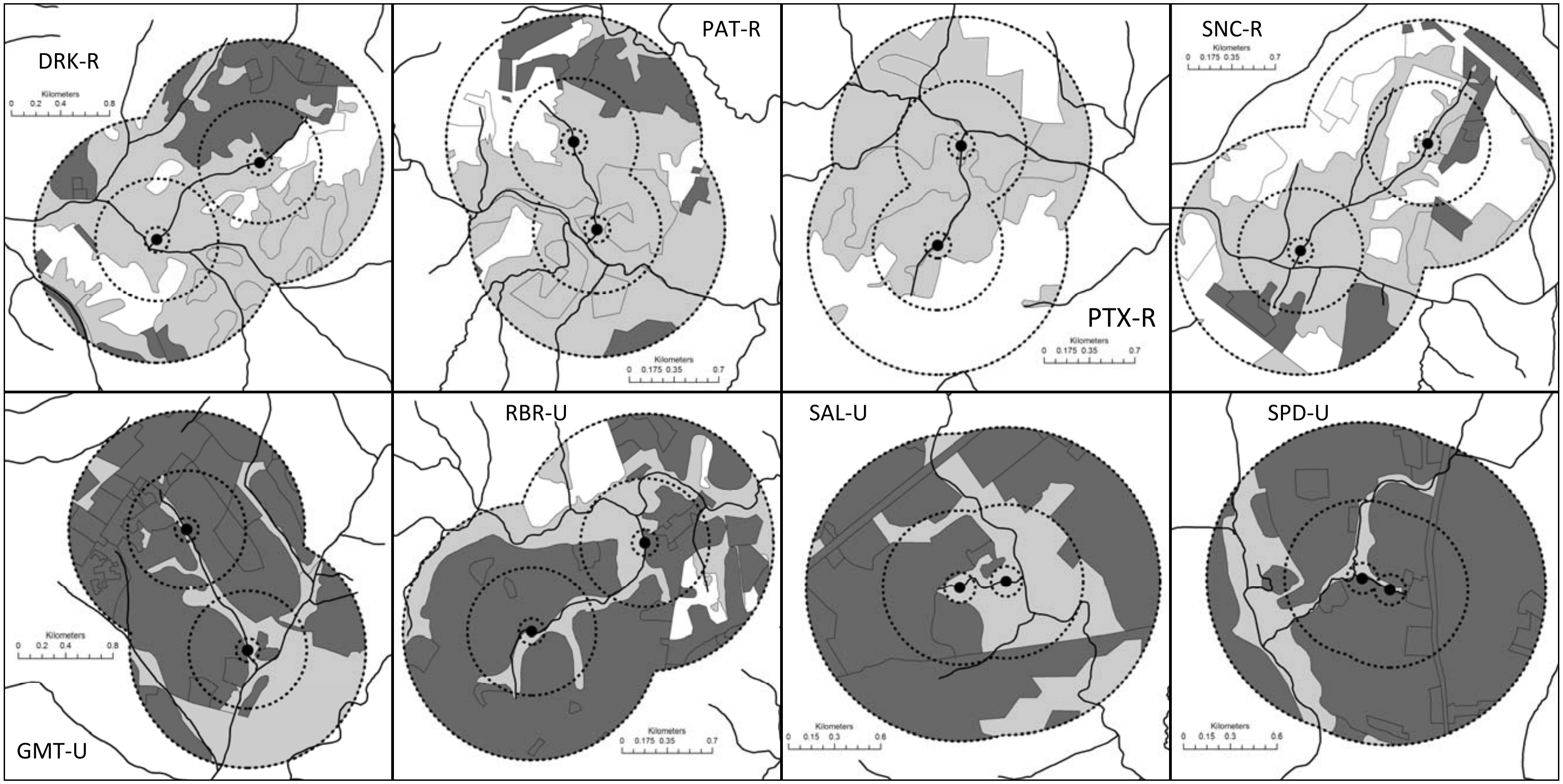


Fig. 3.7. Land use within .1, .5, and 1km radii around the Malaise trap sampling sites at each headwater stream. The top row includes the rural headwaters and the bottom row includes the urban headwaters. The dashed lines represent the boundaries of the radii. Within the dashed lines, the dark grey area represents urban land use, the light grey area represents forested land use, and the white areas represent agricultural land use. Streams are represented by solid black lines.

Gender ratios of immigrants

The percent of the immigrant group that was female generally differed between rural and urban headwaters. The immigrant group was greater than 50% female at 3 rural streams and 49.3% at the 4th stream (PAT) (Fig. 3.9). The immigrant group was greater than 50% female at only 1 urban stream (Fig. 3.9). Thus, the immigrant group at 3 of 4 urban streams had a male bias.

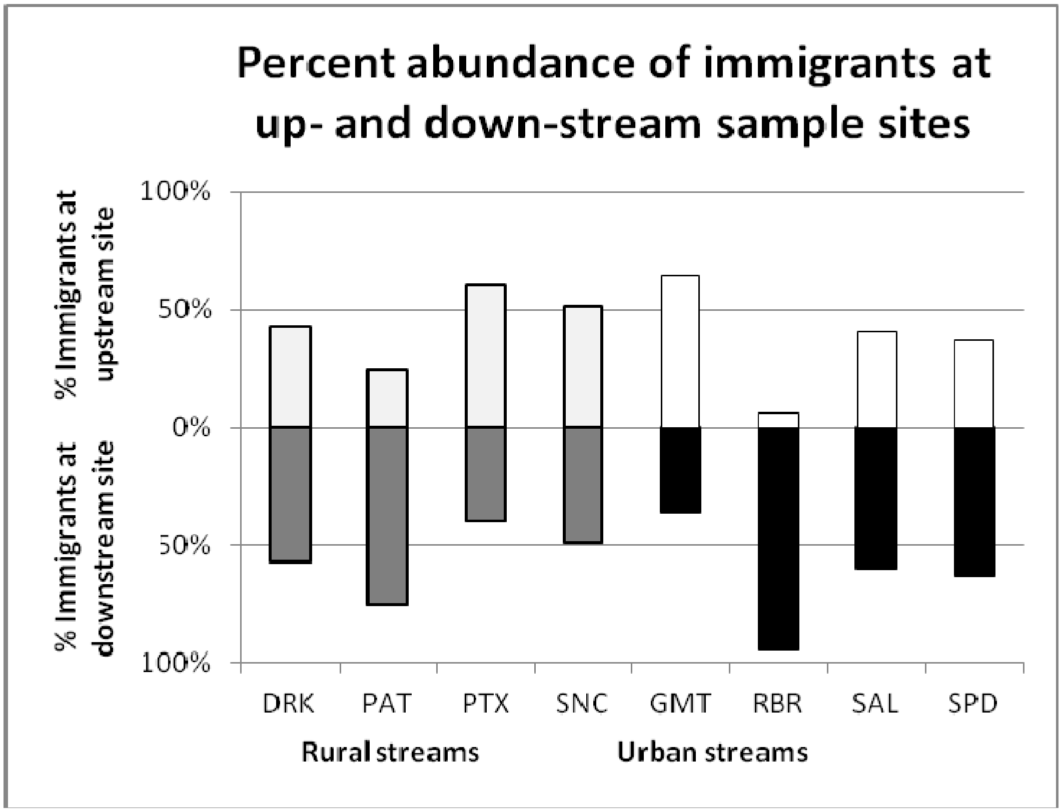


Fig. 3.8. Percentage of immigrants caught at the upstream and downstream sample site locations at each stream.

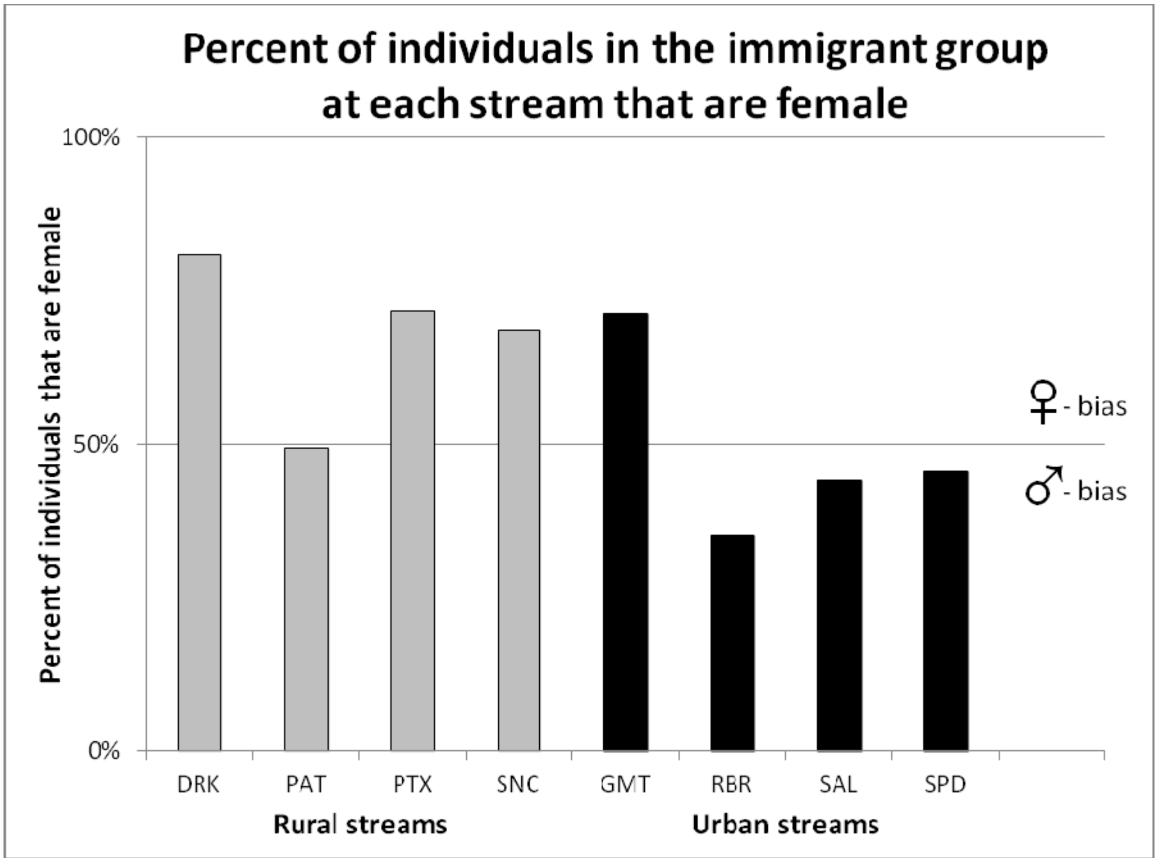


Fig. 3.9. Percentage of immigrants to each site that were female. Grey bars represent the rural headwaters and the black bars represent the urban headwaters. Percentages above 50% indicated the immigrant population is more female than male and below 50% indicated the immigrant population is more male than female.

Discussion

Regional (dispersal mediated) processes interact with local (habitat mediated) processes to determine species presence/absence and community composition (Roughgarden 1989). Altering natural landscapes for human use can cause habitat fragmentation, decrease the permeability of inter-patch environments, and lower the suitability of the remaining habitat patches (Paul and Meyer 2001, Pickett et al. 2001, Fagen 2002, Elmore and Kaushal 2008). The results of this study suggested that changes to aquatic and terrestrial environments resulting from urbanization alter the regional and local processes controlling the composition of the caddisfly assemblage. Patterns of taxa richness and community composition for the adult and larval caddisfly assemblages at rural and urban headwaters indicated that dispersal constraints and in-stream habitat quality were simultaneously causing taxa loss from urban headwaters.

Patterns of adults and larvae between rural and urban streams

Patterns of adult caddisfly taxa richness indicated that dispersal constraints contributed to larval taxa loss from urban headwater streams. The framework for using adult richness patterns to determine the processes controlling larval taxa loss (Fig. 3.1) made the assumption that larval richness was lower at urban than rural headwaters, and this assumption was supported. Based on the framework described in Fig. 3.1, the decreased adult taxa richness at urban headwaters suggested that dispersal by adult caddisflies was constrained in urban landscapes, and constrained dispersal contributed to lower larval richness in urban headwaters. The observed higher % embeddedness, conductivity, and in-stream water temperatures indicated that urban streams had poor in-stream water and habitat quality (Roy et al. 2003) (Tables 2.3 and 2.4, and Fig. 2.3 in chapter 2). In addition, a large amount of empirical work has shown that low in-stream water and habitat quality resulting from watershed urbanization contributes to low larval insect diversity in urban streams (see reviews by Paul and Meyer 2001; Walsh et al. 2005). Dispersal constraints in urban landscapes that prevent immigration by adults act as an additional factor that can prevent colonization and cause lower larval richness in urban streams.

Urbanization altered the way that presence/absence of individual species are controlled by local and regional processes. Decreased richness in urban headwaters resulting solely from the loss of a specific subset of pollution intolerant taxa from the rural headwaters would result in similar taxonomic composition between immigrant groups at urban and rural headwaters. In addition, the loss of a specific subset of taxa would result in the urban resident group consisting of a subset of the taxa from the resident group at rural headwaters. The results of the CA examining the composition of immigrant and non-immigrant groups (Fig. 3.5) indicated that the urban immigrant group was a mix of taxa found in the rural immigrant and rural resident groups. Thus, some taxa that typically immigrated to rural headwaters were constrained from dispersing to urban headwaters, and some taxa belonging to the resident group at rural streams were able to migrate to urban streams but unable to colonize them due presumably to poor in-stream environmental conditions (i.e., shifted to the immigrant group at urban headwaters). The CA indicated that the urban resident group differed from the rural resident group, but this difference was likely due to increased abundance of pollution tolerant larvae supporting high adult abundances (Paul and Meyer 2001, Smith and Lamp 2008). All 10 taxa belonging to the resident group at urban streams were also part of the resident group at 1 or more rural headwaters, and 6 taxa were part of the resident group at all 4 rural headwaters. Thus, the resident group at urban headwaters was largely a subset of the resident group at rural headwaters. The change in species assigned to resident and immigrant groups between urban and rural streams and the composition of the urban resident groups suggested that loss of larval taxa from urban headwaters resulted both from changes to the local and regional processes affecting individual taxa and the loss of taxa with pollution intolerant larvae from poor quality urban headwaters (Urban et al. 2006).

Patterns of adults and larvae between urban streams

The effects of regional and local processes for determining larval richness also differed between taxa found at urban headwater streams. Analysis of assemblage composition did not identify any taxon with a pollution tolerant larval stage (i.e., a resident at some urban headwaters) that was consistently absent from all urban streams as an adult (Fig. 3.5, Table 3.1). Some caddisfly taxa, however, were present as larvae and adults (i.e., resident group) at a subset of the urban headwaters and were completely absent from some of the other urban headwaters. For example, *Diplectrona modesta* gr. (taxon #8, Fig. 3.5, Table 3.1) was part of the resident group at GMT and RBR, was part of the immigrant group at SAL, and was absent at SPD. *Lype diversa* (taxon #30, Fig. 3.5, Table 3.1) was part of the resident group at GMT, was part of the immigrant group at RBR and SAL, and was absent from SPD. High conductivity measures at SAL indicated that this stream was impacted by human activities (Tables 2.4) (Roy et al. 2003), but the habitat and water chemistry data collected in chapter 2 did not indicate that GMT was less impacted than the other urban headwaters (Tables 2.3 and 2.4). Dispersal constraints contributed to the absence of these two taxa from the larval assemblage at SPD, and poor environmental conditions in the stream prevented colonization at SAL. The lack of immigration to an urban headwater, however, does not rule out the possibility that habitat and water quality were also too poor to allow colonization by this species. *Ceratopsyche bronta* (taxon #5, Fig. 3.5, Table 3.1) and *Wormaldia moestra* (taxon #27, Fig. 3.5, Table 3.1) were the other 2 taxa with tolerant larvae that were absent from some urban headwaters presumably due in part to dispersal constraints and absent from others due to in-stream environmental conditions.

Caddisfly taxa that were residents at some urban headwaters and immigrants to the rest apparently did not experience constrained dispersal and were absent because of poor environmental conditions locally in the stream. *Glossosoma nigrior* (taxon #4, Fig. 3.5, Table 3.1) and *Dolophilodes distinctus* (taxon #26, Fig. 3.5, Table 3.1) were part of the resident group at GMT and RBR and part of the immigrant group at SAL and SPD. Some difference in in-stream environmental conditions at SAL and SPD versus GMT and RBR presumably prevented colonization, and in this case, local conditions in the stream were solely responsible for the lack of colonization at SAL and SPD for *G. nigrior*. and *D. distinctus*. The habitat and chemistry data reported in chapter 2 (Tables 2.3 and 2.4) provided only a weak indication that the in-stream conditions were more impacted by human activities at SAL and SPD than GMT and RBR. SAL had the highest conductivity (Roy et al. 2003), SPD has an unusually high amount of embeddedess at the upstream location, and both streams were dominated by run and/or pool habitat (Tables 2.3 and 2.4). The environmental conditions that prevented colonization at SAL and SPD were possibly impacts from human activities not measured in chapter 2 (e.g., hydrologic alterations) or were natural differences between the streams. *Hydroptila* spp. (taxon #11, Fig. 3.5, Table 3.1) was the other taxon with tolerant larvae that was absent from some urban headwaters due solely to in-stream environmental conditions. *Hydroptila* spp. typically inhabits larger streams (i.e., the main-stem) in Maryland's Piedmont (Smith 2006), and natural conditions in headwaters rather than the poor conditions due to land use urbanization may have prevented colonization for this taxon.

The patterns of presence and absence at urban headwaters showed that both regional and local processes may have determined community composition within a single stream. Local habitat was potentially responsible for the absence of 3 taxa (*G. nigrior* and *D. distinctus*, and *Hydroptila* spp.) and regional dispersal constraints potentially contributed to the absence of 4 taxa (*D. modesta* gr., *L. diversa*, *C. bronta*, and *W. moestra)* from SPD (Fig. 3.5, Table 3.1). The roles that regional and local processes play in determining community composition of urban streams likely differ between streams based on site specific characteristics.

Radial land use analysis

Amount of immigration to urban streams examined in this study was related to land use surrounding the stream at small spatial scales. The greatest abundance of immigrants to an urban headwater stream occurred at SAL, and this site had the lowest amount of urban land use in the 0.1 and 0.5km radial buffers of all the urban headwaters. The configuration of urban land use evident in Fig. 3.7 showed that a large area of forested land existed around the adjacent main-stem stream to SAL. This area may have unmarked tributaries and/or ephemeral streams that supply immigrants (Meyer et al. 2007). Dispersal at this small spatial scale still represents a regional process. Physical and behavioral adaptations for strong dispersal ability for species inhabiting ephemeral and/or headwater habitats may have contributed to small streams serving as sources of migrants (Fahrig and Merriam 1994, Wilcock et al. 2007). In addition, species with tolerant larvae may not have experienced dispersal constraints because their larvae persisted in nearby poor quality source habitats (Lowe 2002).

Larger areas of non-urban land use also occurred around the downstream locations at RBR and GMT. The downstream location at RBR possessed 94.1% of the total individuals that immigrated to that stream, and small unimpacted streams nearby may have supplied a high amount of immigrants to that downstream location. Contrary to what occurred at RBR, more immigrants were found at the upstream location at GMT. Natural variation in the structure of remaining non-urban habitat or variation in the structure of the urban landscape between GMT, RBR, and SAL may have contributed to the observed differences in immigration (Fahrig 2007).

Upstream/downstream comparison of immigrants

Patterns of upstream versus downstream abundance for the immigrant group can indicate if the immigrant taxa are migrating upstream from the mouth of the headwater (Macneale et al. 2004). No obvious differences in up and downstream abundance patterns for taxa in the immigrant group existed between urban and rural streams. More immigrants were caught at the downstream trap at 3 of the 4 urban streams, but only RBR deviated strongly from a 50:50 ratio for up and downstream abundance. The patterns of immigrants were similar to those observed for the entire community (Fig. 2.10a, chapter 2). The high abundance of the immigrant group at the downstream sample site at RBR suggested immigration may have occurred through the stream corridor for this stream, but the lack of a strong longitudinal difference in abundance at the other streams provided weak support for adult dispersal occurring through upland areas (Petersen et al. 2004).

Gender ratios

The difference in gender ratio for the immigrant groups between urban and rural streams suggested that some aspect of the urban landscape caused a male bias in the immigrant group to urban headwaters. The gender ratio of the immigrant group at the urban headwater was more male biased than the immigrant group to rural headwaters and what was found for the entire caddisfly assemblage at urban and rural streams reported in chapter 2. Decreased females in the immigrant group could have amplified the effect of dispersal constraints contributing to low diversity of the larval assemblage at urban headwaters. Females are directly responsible for supplying recruits for the next generation, and high female abundance is associated with a high probability of colonization (Ahlroth et al. 2003). A male bias in the migrant groups to urban headwaters may have further limited the ability of dispersers to contribute to recruitment and may represent an additional regional processes contributing to taxa loss from urban headwaters. Very few females, however, are needed to supply enough recruits for a population to persist (Bunn and Hughes 1997), and the lack of female immigrants to urban headwaters may not substantially impact presence/absence of larval taxa.

Rural headwaters

A combination of local and regional processes most likely worked simultaneously to determine assemblage composition at rural streams as well. Not all taxa in the regional pool migrated to each rural headwater, and many taxa of adults found at some rural streams failed to colonize other streams due presumably to local factors (i.e., in-stream habitat) (Fig. 3.5). The larval assemblages in rural headwaters were most likely structured primarily by the local environment (Heino et al. 2003b). Constraints on dispersal and colonization were likely lower at rural than urban streams and contributed less to the process structuring the larval caddisfly assemblages at rural than urban streams; but the overall results suggested that local and regional processes worked simultaneously at rural headwaters (Cottenie and De Meester 2005, Driscoll and Lindenmayer 2009, Brown and Swan 2010).

Support for metacommunity perspectives

The importance of local and regional processes for structuring communities varies between the four metacommunity paradigms (patch dynamics, species-sorting, mass-effect, and neutral) (Leibold et al. 2004). The results of this study indicated that local and regional processes occurred simultaneously, thus supporting a situation where multiple metacommunity paradigms explain assemblage composition at urban and rural headwater streams (Cottenie and De Meester 2005, Driscoll and Lindenmayer 2009, Brown et al. 2011). The species specific and site specific differences in the importance of local and regional processes between urban streams suggested that the other metacommunity perspectives based on dispersal could explain patterns for certain species at certain streams.

This study directly compared the adult and larval assemblages at individual headwater streams to determine patterns of immigration and colonization rather than indirectly assess the metacommunity perspectives (i.e., local versus regional processes) by examining the relationships between geographic distance and environmental dissimilarity to community dissimilarity (Chase 2005). The sampling methods employed in this study did not provide any information on emergence from the stream, and thus I could not document a mass effect (Leibold et al. 2004). My results however, supported the findings of other studies examining distance-similarity relationships that multiple paradigms acted concurrently within metacommunities (Cottenie and De Meester 2005, Driscoll and Lindenmayer 2009, Brown and Swan 2010). The advantage to my study is that species and site specific differences could be determined for the 8 streams included in the study.

Applications for restoration

The results of this study have direct applications to the conservation and restoration of stream ecosystems. Current methods for analyzing biological condition of a stream ecosystem focus on finding correlates between the larval community, in-stream water and habitat quality, and watershed land use (Bonada et al. 2006). The results of this study suggested that regional processes may play a secondary, but important role in determining the composition of the larval community in urban streams. Including the landscape level factors controlling isolation or dispersal constraints may improve interpretations of bioassessments (Heino et al. 2003a), but more work is needed to identify these factors and how to implement them into bioassessment analyses.

The data collected in this study also indicated that urban streams were not completely isolated. Numerous taxa of adult caddisflies (3 to 14 taxa) belonged to the immigrant group at urban headwater streams, and the immigrant group accounted for at least half of the adult assemblage at urban headwaters (50% to 82.4%). Some taxa of the immigrant group to the urban headwaters had low adult abundance (classified as rare immigrants in Fig. 3.5); and taxa with low adult abundance may also have low larval abundance, which may decrease larval detectability in urban streams. The number of taxa in the immigrant groups with high adult abundances represented 28.6%, 31.6%, 52.9% of the total adult assemblage at GMT, RBR, and SAL respectively, and these percentages still indicated that urban headwaters were not completely isolated. The low level of immigration to SPD suggested however, that some streams may be severely isolated from potential source populations. While some dispersal constraints existed, the level of immigration observed at most of the urban streams indicated that restoring these streams may lead to successful colonization by many caddisfly taxa, and richness could at least double if all immigrants successfully colonized the stream (Table 3.2).

A priori determination of colonization potential is important for planning a successful stream restoration project (Bond and Lake 2003). Restoration projects often work under the "field of dreams" hypothesis that taxa will colonize any habitat that is built (i.e., restored) over time (Palmer et al. 1997, Bond and Lake 2003, Lake et al. 2007). Poor in-stream environmental conditions may be the primary cause of low larval diversity in streams impacted by human activities and should be the focus of restoration projects. Dispersal constraints occurring in urbanized landscapes, however, may contribute to low diversity and may prevent some individuals from colonizing a restored stream reach (Brown et al. 2011). Immigration levels differed between the 4 urban headwater streams included in this study, and the observed differences were linked to land use patterns at small spatial scales. The factors controlling immigration can differ between stream reaches, and a site by site approach that examines landscape characteristics and the regional species pool may be required to determine the colonization potential by stream insect to candidate restoration sites.

Determination of colonization potential through field studies of immigration rates or analyses of landscape factors that indicate the composition, richness, and dispersal abilities of potential migrants can improve restoration projects but may be difficult to develop (Hughes 2007, Lake et al. 2007). The utility of predicting colonization potential through field studies will differ between species, but may be a useful tool for stream insects given ontogenetic shifts in habitat utilization between larval and adult stages (Purcell et al. 2002). A more fruitful method for predicting colonization success at the community level may be to assess the landscape level characteristics related to colonization potential using GIS. Chapter 1 synthesized information about the potential dispersal constraints faced by stream insects in urban landscapes. Studies like this may be the basis for developing GIS based analysis tools to predict potential colonization, but more empirical work is needed to understand the impacts of urbanized landscapes on adult stream insects. Any tool that predicts colonization success will help identify appropriate endpoints, evaluate project success, and better utilize available funds for stream restoration projects.

Summary

The overall patterns of adult richness and abundance at urban and rural headwater streams suggested that local and regional processes worked simultaneously in a hierarchical manner to cause species loss from urban headwaters. Dispersal constraints acted first on a subset of the taxa, and poor water and habitat quality acting secondarily on the majority of caddisfly species (Patrick and Swan 2011). Species specific differences in the response to the prevailing conditions in the stream and at the landscape scale likely caused the importance of local and regional processes for controlling assemblage composition to differ between urban streams. In addition, urban landscapes may have altered the sex ratios of immigrants to urban streams, which could alter colonization rates and contribute to lower larval diversity in urban headwaters (Ahlroth et al. 2003). The results of my study suggested that dispersal constraints experienced by adults, the geographic location of source populations, and spatial characteristics of the urban landscape are additional filters at the landscape scale that may alter regional processes structuring communities in urban headwater streams (Poff 1997, Patrick and Swan 2011).

Chapter 4: Relation of flight morphology traits of adult caddisflies (Trichoptera) to dispersal through urban landscapes

Abstract

Dispersal is important for population persistence and maintaining community diversity. Morphological traits related to flight may play an important role in allowing species to migrate through harsh urban landscapes to isolated stream ecosystems. My objective was to compare wing length and wing aspect ratio between 6 caddisfly species representing 3 groups that differed in their level of immigration to urban headwater streams based on a previous survey of adult and larval caddisflies. I hypothesized that wing length and aspect ratio were lower for the taxa that did not migrate to urban headwaters. Fore and hindwing length and width were calculated from digital images of dissected wings from 7-20 males and 10-20 females of each species. While significant differences existed between species for forewing length, forewing aspect ratio, and combined aspect ratio (females $p<0.0001$, males $p<0.0001$ for all three measures), the 2 non-migrant species did not possess the lowest wing length or aspect ratio for males or females of the 6 species analyzed. A tradeoff between wing size/shape and body size was evident for 2 species of immigrants. *Ptilostomis ocellifera* had the longest wings, was largest bodied species, and had the lowest wing aspect ratio. *Lype diversa* had the shortest wings, was the smallest bodied species examined, and had the highest wing aspect ratio. Being large bodied with high energy stores or small bodied with an efficient

wing design can aid dispersal by flight, and these morphological characteristics may have supported dispersal through urban landscapes by these 2 species. The importance of wing size and aspect ratio for supporting dispersal through urban landscapes may be species specific, but other morphological characteristics related to flight and the spatial locations of source populations may also determine dispersal patterns through urban landscapes.

Introduction

The act of dispersing from one habitat to another includes the specific process of leaving a patch, moving between patches, and entering (and remaining in) a different habitat patch (Ims and Yoccoz 1997). Physical attributes related to the mechanics of insect flight and the amount of available energy resources required for flight determine the physical ability for insects to fly between patches. High muscle content in the thorax indicates strong wing movements, and energy stores, in the form of lipids, determine flight duration (Elliott and Evenden 2009). These factors interact with the structural aerodynamics of insect wings and overall body size to determine flight ability. For example, the larger the ratio of the organism’s body to its wing size, the more energy is needed for flying (Byrne et al. 1988, Lindhe Norberg 2002). Wing aspect ratio (wing length / wing width) is also related to the energy needed for flight. Reduced energy use from lower drag created by wings with a high aspect ratio (length / width) makes them more aerodynamically efficient than short, wide wings (Vogel 1981). Species with high wing aspect ratios are suited for long distance flights since less energy is required to remain flying (Altizer and Davis 2010). Wing coupling (the movement of fore and hind wings together during the wing stroke) allows for greater aerodynamic efficiency by eliminating the decrease in lift that can occur when pairs of wings act independently, and this adaptation may support strong dispersal ability as well (Wooton 2002).

The dispersal of individuals between habitat patches impacts population and community level processes related to occupancy, abundance, gene flow, and diversity (Bilton et al. 2001, Fagen 2002, Lowe 2002); and as a result, the morphological characteristics associated with insect flight can impact population and community dynamics. Flight ability can affect insect survival by impacting resource acquisition, predator avoidance, or mate finding behaviors (Bilton et al. 2001, Almbro and Kullberg 2008). Dispersal from one patch to another is based on behavioral and physical traits related to flight that interact with environmental conditions in the habitat patch, the patch edge, and the matrix between the patch (Ims and Yoccoz 1997). While multiple factors determine dispersal ability, the physical traits related to flight are an important determinant of a species ability to move between habitat patches. The relationship of morphological characteristics associated with strong flight ability to population presence/absence and greater population range sizes suggests that dispersal is dependent on flight ability (Hoffsten 2004, Rundle et al. 2007). Thus, interspecific differences in species traits related to flight may help to explain patterns of community diversity across the landscape.

The geographic features of the landscape such as spatial scale, inter-patch distance, and matrix permeability determine the dispersal ability needed for population persistence, which can impact patterns of diversity within and across patches (Leibold et al. 2004, Cadotte 2006). Species traits related to strong flight ability are opposed by large scale environmental gradients and landscape structures that make dispersal difficult. For example, poor dispersers may expand throughout contiguous, highly permeable habitats over long temporal scales, but good dispersers may not move through poor quality matrix habitats and colonize isolated patches of good habitat that are geographically close together. Strong flying species (based on the physical characteristics related to flight), however, are more likely to move longer distances through inhospitable environments than species that are weak fliers (Sanderson et al. 2005).

Strong dispersal may be particularly important for flying through urban landscapes. Urban land separating stream ecosystems can increase mortality, decrease fitness, or constrain dispersal for adult stream insects (chapter 1). Strong flight ability may lessen the constraints on adult stream insects moving through urban landscapes. Morphological features related to efficient flight may allow individuals to move over or around physical structures that block dispersal (Blakely et al. 2006) or continue to disperse after being distracted by environmental sinks (Kriska et al. 2008, Perkin et al. 2011). Strong dispersal ability may also allow taxa to successfully move the long distances between habitat patches in a fragmented urban landscape (Fahrig and Merriam 1994, Fagan 2002). Headwater habitats in particular are experiencing the greatest amount of habitat destruction in urban landscapes, and habitat destruction results in increased distances between remaining headwater reaches (Elmore and Kaushal 2008). Interspecific differences in flight ability interact with landscape scale features of urban landscapes to determine the ability to disperse between locations (Fahrig 2007), and thus, flight ability may partly determine the composition of species assemblages.

This study examined if wing morphological characteristics related to flight differed between 4 headwater caddisfly species that were observed migrating to urban streams (migrants) versus 2 species that did not (non-migrants) in a previous survey of adult and larval caddisflies at urban and rural headwater streams (chapter 3). Wing length and wing aspect ratio were compared between caddisfly species from the migrant and non-migrant groups. I hypothesized that non-migrant species had smaller wings and smaller wing aspect ratios than the migrant species. Comparisons of wing length and aspect ratio were done for females and males separately based on the *a priori* assumption that sexual dimorphism of wing morphology existed for caddisflies.

Methods

Species selection

Previous work comparing the adult and larval caddisfly assemblages at rural and urban headwater streams showed that urban headwaters were not isolated and received immigrants, but not all the taxa in the regional species pool migrated to urban headwaters (chapter 3). Differences in flight morphology should occur between groups with different observed levels of immigration to urban streams if flight ability is a factor controlling movement through urban landscapes. An assessment of the importance of physical flight ability for migrating to urban streams can be made by comparing the physical traits related to flight ability between taxa that exist on opposite ends of an observed immigration gradient.

Morphological characteristics were compared between the 2 most abundant species from 3 groups of species representing different levels of immigration using the collections from chapter 2 of this dissertation. The three groups of species compared were: Group I – the 2 most abundant species that were present as larvae and adults at rural headwaters but were not found as adults at urban streams where their larvae were absent (i.e., non-immigrants); Group II – the 2 most abundant species that were present as larvae and adults at rural headwaters and were found as adults at urban streams where their larvae were absent (i.e., immigrants); and Group III – the 2 species that were present as larvae and adults at rural headwaters, present at a subset of the urban headwaters, and had the greatest abundance of adults at the other urban headwaters that lacked their larvae (i.e., occasional immigrants). The species selected for Group I were the 2 species with the highest abundances of adults at rural headwaters that fit the criteria. The species selected for Group II were the 2 species with the highest abundance of adults at urban headwaters that fit the criteria. The species selected for Group III were the 2 species with the greatest abundance of adults at the subset of streams where their larvae were absent that fit the criteria. These groups are referred to as GI-NonIM (group I, non-immigrants), GII-IM (group II, immigrants), and GIII-OccIM (group III, occasional immigrants) in the remainder of this chapter (Table 4.1 and Table 4.2). Data on adult and larval abundances presented in chapters 2 and 3 were used to determine which species best fit the 3 groups described above.

Psilotreta frontalis (Odontoceridae) and *Rhyacophila carolina* (Rhyacophilidae) were the two species selected for GI-NonIM (Table 4.2). Adult *P. frontalis* had a total standardized abundance of 158.8 individuals and adult *R. carolina* had a total standardized abundance of 128.3 individuals across all 10 weeks of malaise trap sampling at rural headwaters (see chapter 2 for description of standardized abundances and Table 2.2 for sampling times). Both taxa where present at all 4 rural sites as an adult and present at 3 of 4 rural sites as larvae. No species fitting the criteria for GI-NonIM were present at all 4 rural streams as larvae and adults.

Polycentropus carolinensis (Polycentropodidae) and *Ptilostomis ocellifera* (Phryganeidae) were the two species selected for GII-IM (Table 4.2). Only genus data were available for larval *Polycentropus*, but no adults of this genus were found at any urban headwater stream. *P. carolinensis* was the most abundant immigrant of all the caddisfly species that fit the criteria for GII-IM when adult abundances of each species of *Polycentropus* were examined individually. Adult *P. carolinensis* had a standardized abundance of 31.6 individuals and adult *P. ocellifera* had a standardized abundance of 15 individuals over 10 weeks of malaise trap sampling at urban headwaters (see chapter 2 for description of standardized abundances and Table 2.2 for sampling times). Both taxa were present as an adult at all 4 rural headwaters and 3 of 4 urban headwaters. Larval *P. ocellifera* was present at 3 of 4 rural headwaters, and larval *Polycentropus* spp. were present in high abundances (standardized total abundance = 1,581.8) across all 4 rural

Table 4.1. List of acronyms referenced in the text.

Methods section	Acronym	Description
Species selection	GI-NonIM	Non-immigrants to urban headwaters (larvae and adults absent from urban headwaters)
	GII-IM	Immigrants to urban headwaters (larvae absent from urban headwaters, but adults present)
	GIII-OccIM	Occasional immigrants to urban headwaters (larvae present at some urban headwaters, but adults present in high abundances at urban headwaters where larvae are absent)
Rationale and methods for morphological measurements	FWL	Forewing length
	FWAR	Forewing aspect ratio (forewing length / forewing width)
	CAR	Combined fore and hindwing aspect ratio (forewing length / forewing + hindwing width)

Table 4.2. Species used in analysis of wing morphological characteristics.

Family	Genus species	Collection location[a]	Group	FFG[b]
Odontoceridae	*Psilotreta frontalis*	PAT(wk10)	GI-NonIM	SC
Rhyacophilidae	*Rhyacophila carolina*	DRK, PTX, and PAT(wk14)	GI-NonIM	PR
Polycentropodidae	*Polycentropus carolinensis*	DRK(wk10)	GII-IM	PR/CF/SH
Phryganeidae	*Ptilostomis ocellifera*	PAT(wk14), DRK(wk14 & 18)	GII-IM	SH/PR**
Philopotamidae	*Dolophilodes distinctus*	PTX(wk14)	GIII-OccIM	CF
Psychomyiidae	*Lype diversa*	PTX(wk6)	GIII-OccIM	SC*

[a] Acronyms used for collection location are described in chapter 2. The week collected is listed in parentheses (see Table 2.2 for dates of collections)

[b] FFG represents the primary functional feeding group(s) listed for the genus that each taxon belonged to from Morse and Holzenthal (2008). * indicates that a species level FFG designation was provided. ** indicates that only facultative FFG designations were listed. FFG abbreviations are CF: collector-filterer, SC: scraper, PR: predator, and SH: shredder

headwaters. The high abundances of adult *P. carolinensis* suggested that this species made up a large percent of the *Polycentropus* larvae rural headwaters, and thus, *P. carolinensis* larval abundances were likely high in unimpacted headwater streams as well.

Dolophilodes distinctus (Philopotamidae) and *Lype diversa* (Psychomyiidae) were the 2 species selected for GIII-OccIM (Table 4.2). Adults of these species were highly abundant at urban streams where their larvae were absent, but presence of their larvae at some urban streams suggested that these species had pollution tolerant larvae capable of inhabiting certain urban headwaters. *D. distinctus* larvae were present at 2 urban headwaters. Adult *D. distinctus* had a standardized abundance of 660 individuals over 10 weeks of malaise trap sampling at the 2 urban headwaters where the larvae were absent. *L. diversa* larvae were present at only 1 urban site, and only a single individual was found at that urban headwater. Adult *L. diversa* were present at 2 of the 3 urban headwater streams that lacked the larvae, and it had a standardized abundance of 68.4 individuals over 10 weeks of malaise trap sampling at these 2 urban streams (see chapter 2 for description of standardized abundances and Table 2.2 for sampling times). *D. distinctus* and *L. diversa* were included because their adult abundances at the subset of urban streams that lacked their larvae were greater than the abundances for the species from GII-IM at urban headwaters. These species had a high propensity for immigrating to urban streams, but larval tolerance to pollution potentially allowed source populations of larval to inhabit nearby urban streams. The possibility that local source populations controlled immigration led to the inclusion of GIII-OccIM as a separate group of species representing immigrants.

Specimen collection

Specimens of adult used for the study were taken from the collections made for chapter 2 of this dissertation. All field methods for collecting adult caddisflies described in chapter 2 apply to the specimens used for analysis in this study. In summary, adult insects were collected in the field using Malaise traps containing 80% ethanol as a preservative. Samples were returned to the lab where all adult caddisflies were removed from the samples and transferred to 100% ethanol and stored at -17°C until analysis.

Specimens used for morphological analysis were taken from samples collected at rural headwaters where their larvae were also present (i.e., they belonged to the resident group) (Table 4.2). Poor quality or highly disturbed aquatic habitats may lead to decreased flight capabilities and alterations to the morphological features related to flight (Stevens et al. 1999, Huryn and Wallace 2000, Jannot et al. 2007, De Block and Stoks 2008). Food quality in urban areas may also affect dispersal ability (Rankin and Burchsted 1992) or the morphological characteristics related to flight (Plaistow and Siva-Jothy 1999). Therefore, individuals from samples collected at urban headwaters were not used for analysis to avoid altered morphological conditions caused by poor environmental conditions. Individuals were only taken from samples collected at locations where their larvae were present to increase the possibility that individuals included were residents that emerged from the natal stream. When possible, specimens used were taken only from samples collected during the period that represented their peak abundance at rural streams to avoid seasonal differences in adult physical traits (Spänhoff 2005, Wagner 2005b). As an exception, specimens of *P. ocellifera* were taken from samples collected across multiple weeks due to the total low abundance of adults at rural streams. Specimens used were taken first from samples collected at rural streams with the highest larval abundance to further increase the likelihood that specimens analyzed were local residents and not immigrants. Specimens were taken from samples collected at other rural streams starting at those with the highest larval abundance to lowest abundance if an insufficient number of individuals were collected in samples taken from the rural headwater with the greatest adult abundance. This protocol, however, does not preclude the use of specimens that immigrated to rural headwaters, which could represent a group of specimens with morphological traits selected for long distance dispersal and not representative of the entire population (Altizer and Davis 2010).

The target abundance for analysis of morphological traits was a total of 20 males and 20 females for each species. The analysis included this number of individuals for *P. frontalis*, *P. carolinensis*, *D. distinctus*, and *L. diversa*. A lack of specimens collected and wing damage during capture and field preservation resulted in 20 males and 19 females being examined for *R. carolina* and 7 males and 10 females being examined for *P. ocellifera*.

Rationale and methods for morphological measurements

Several morphological characteristics are related to flight ability in adult caddisflies. Low wing loading (total body mass / total wing area) (Byrne et al. 1988, Lindhe Norberg 2002) and high flight muscle ratio (ratio of pterothorax to whole body mass) are associated with a greater ability for flight in insects (Marden 2000, Berwaerts et al. 2002). Wings with a high aspect ratios (i.e., long skinny wings) require less energy to remain airborne, which makes them more aerodynamically efficient than low aspect ratio wings (Vogel 1981); and high wing aspect ratios are correlated with long distance dispersal by flying insects (Altizer and Davis 2010). In addition, wing length is correlated with body size (Petersson 1989, Goretti et al. 2005), and larger wing length and larger overall size indicate greater dispersal ability (Malmqvist 2000, Hoffsten 2004, Rundle et al. 2007). Small bodied organisms, however, may disperse long distances aided by the wind (Bilton et al. 2001). Thus, both large and small bodied individuals may be strong dispersers.

The use of field collected specimens for analysis restricted the measurements used in this study to those that do not include body mass or body length. Collection and storage in ethanol can change a specimen's total length from the contraction of body segments (in particular the abdomen), and storage in ethanol may cause certain constituents of the body to "leach" out, which may alter dry mass (Benke 1996). Leaching of body constituents prevents an accurate estimation of true body mass, and distortions of total body length alter the effectiveness of estimating dry mass from body length measurements. Collection and preservation methods used in this study do not alter wing size and shape, and as a result, wing aspect ratio and wing size were used in this study to estimate flight ability. Greater wing aspect ratio and greater wing size were considered indicative of greater flight ability (Vogel 1981, Malmqvist 2000, Hoffsten 2004, Rundle et al. 2007, Altizer and Davis 2010).

The fore and hindwings were removed from the right side (from dorsal view) of each specimen. The left side wings were used if either of the right side wings were damaged and morphological measurements were not possible. Wings were dissected using forceps and a scalpel. Excess tissue (e.g., wing muscles) was removed from the wing base, and the fore and hindwings were wet mounted on a microscope slide under a coverslip. Slides were placed on a gridded background to use as a spatial reference for performing measurements. Measurements were done on a digital image taken of each pair of wings using a Canon EOS 20d digital camera with a 60mm 1:2.8 macro lens (Canon USA, Inc.).

Wing length and width were determined using the program ImageJ v1.45s (National Institutes of Health, USA). Wing length was measured first along a line from the base of the wing to the tip. The width of the wing was measured at the widest part of the wing along a line perpendicular to the line used to calculate length. Wing venation and other features of the wing were used as references for measuring wings within a species, but not all measures were done at the exact same location along the wing since wing shape occasionally varied between individuals within the same species.

The variables calculated from these measures were forewing length (FWL), forewing aspect ratio (FWAR), and combined fore and hindwing aspect ratio (CAR) (Table 4.1). FWL was used as the measure of wing length since forewings are longer than hindwings for all the species analyzed in this study. FWAR was the length of the forewing divided by the width of the forewing, and CAR was the length of the forewing divided by the sum of the widths of the fore and hindwings. Most taxa of Trichoptera employ some form of wing coupling during flight (Wooton 2002, Stocks 2010). Either wings are physically connected together or the fore and hindwings move together during the wing stroke (Stocks 2010). Measures of wing aspect ratio using the combined widths of the fore and hindwings are appropriate for taxa that employ wing coupling (Hoffsten 2004). Philopotamidae is a family of Trichoptera that does not employ any wing coupling (Stocks 2010), and as a result, comparing *D. distinctus* using a wing aspect ratio values calculated from the sum of the fore and hindwing widths may not be appropriate. As a result, both FWAR and CAR were included in the analysis.

Statistical analyses

Morphological measures of wing length and aspect ratio were compared between species for males and females separately. Sexual dimorphism in overall size and wing size is common in caddisflies (Goretti et al. 2005, Spänhoff 2005). The interspecific comparisons of wing morphological characteristics were done separately for females and males based on the *a priori* expectation that wing shape may differ between genders as well. Comparisons of morphological characteristics were done between males and females for each species to determine if the *a priori* assumption was valid using individual t-tests for each species. The residuals were normally distributed for all comparisons except for the measure of FWAR for *P. frontalis* (R version 2.14.1; *Shapiro.test* protocol; *stats* package 2011). In this case, a single outlier for the female measurements caused the distribution of the residuals to be slightly skewed. There was no valid reason to remove the outlier, and all the other measures conformed to the assumption of normality so the analysis was performed on the original data. Heterogeneous variances were found in 8 of the 18 total tests of all 3 morphological variables across all species using Bartlett's test of homogeneity of variances in R version 2.14.1 (*bartlett.test* protocol; *stats* package 2011). Comparisons were done using Welch's t test for unequal variance when variance was heterogeneous, and comparisons were done using a student's t test when variances were homogenous (R version 2.14.1; *t.test* protocol; *stats* package 2011).

Comparisons of morphological characteristics between taxa for each gender were done using an analysis of variance (ANOVA). The residuals were normally distributed for all comparisons (R version 2.14.1; *Shapiro.test* protocol; *stats* package 2011). Bartlett's test of homogeneity of variances (R version 2.14.1; *bartlett.test* protocol; *stats* package 2011) showed that the data for all but 2 comparisons (FWAR and CAR for females) had heterogeneous variances, and the two cases with homogeneous variances had high Bartlett's K-squared values (FWAR-female = 10.304, p = 0.067 and CAR-female = 9.648, p = 0.086). Heterogeneous variances were considered a systemic problem for comparisons of all morphological characteristics between species for males and females. As a result, the ANOVA performed for each analysis partitioned the variance within each species (i.e., treatment) using a mixed model (Proc mixed) where the *repeated* option is used to partition the variance within species. Adjusted error rates for pairwise comparisons between species were calculated using Dunnett's T3 method (Dunnett 1980). The ANOVA was performed using SAS statistical software version 9.1 (SAS Institute Inc., Cary, NC, USA).

Results

Differences between males and females

Morphological characteristics related to flight were significantly different between males and females for most species examined. FWL was significantly different between females and males for all 6 species analyzed at an alpha of 0.05 (Fig. 4.1). Variance for FWL was very low for all 6 species, and was highest for male *P. ocellifera*. FWAR was significantly different between females and males for all species except *L. diversa* (t = -0.804, df = 31.31, p = 0.43) (Fig. 4.2). Variance was low for this measure, and was highest for male *L. diversa*. CAR was significantly different between females and males for all species except *P. ocellifera* ($t = 1.639$, $df = 15$, $p = 0.12$) and *L. diversa* ($t = -1.852$, $df = 30.82$, $p = 0.07$) (Fig. 4.3). Variance was low for this measure as well, and was highest for male *L. diversa*.

Species differences

The ANOVA found a significant difference between species for females ($F_{5,37.7} = 2608.2$, $p<0.0001$) and males ($F_{5,30.4} = 1241.8$, $p<0.0001$) for FWL (Fig. 4.4). The pattern for differences between species was the same for both females and males. *P. carolinensis* was not significantly different than *D. distinctus*, and had the second shortest wings of all 6 species (Fig. 4.4). *P. ocellifera* had the longest forewing and *L. diversa* the shortest forewing. *P. frontalis* and *R. carolina* (GI-NonIM) had the second and third longest wings of all 6 species for females and males. There were no consistent differences between species groups for either gender.

The ANOVA found a significant difference between species for females ($F_{5,42.7} = 195$, $p<0.0001$) and males ($F_{5,34.4} = 144.1$, $p<0.0001$) for FWAR (Fig. 4.5). Female *P. frontalis* was not significantly different from female *R. carolina*, and female *P. carolinensis* was not significantly different from *D. distinctus* (Fig. 4.5a). Male *P. frontalis* was not significantly different from male *P. carolinensis* (Fig. 4.5b). *L. diversa* had the highest FWAR for females and males, and *P. ocellifera* had the lowest FWAR for females and males. *R. carolina* (GI-NonIM) had the second smallest FWAR for both males and females. *P. frontalis* (GI-NonIM) females had the second smallest FWAR, and the males had the third smallest FWAR. In fact, male *P. frontalis* had the 2nd highest

FWAR of all 6 species (though not significantly different from *P. carolinensis* of GII-IM). There were no consistent differences between species groups for either gender.

The ANOVA found a significant difference between species for females ($F_{5,43.2}$ = 680.1, *p*<0.0001) and males ($F_{5,35}$ = 375.1, *p*<0.0001) for CAR (Fig. 4.6). Female *P. frontalis* was not significantly different from female *D. distinctus*, and female *P. carolinensis* was not significantly different than *D. distinctus* (Fig. 4.6a). Male *P. frontalis* was not significantly different from *D. distinctus* (Fig. 4.6b). Similar to FWAR, *L. diversa* had the highest CAR for females and males, and *P. ocellifera* had the lowest CAR for females and males. *R. carolina* and *P. frontalis* (GI-NonIM) had the second and third smallest CAR respectively for both males and females. There were no consistent differences between species groups for either gender.

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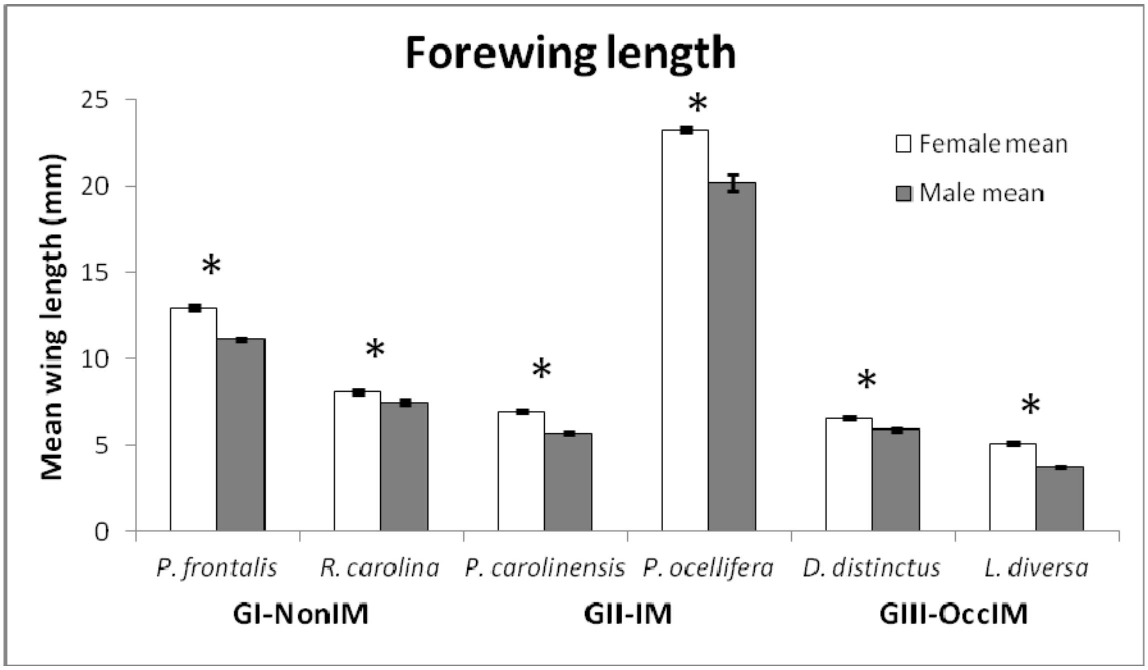


Fig. 4.1. Mean (±1 SE) wing length for females (white) and males (grey) for each species. An asterisk represents a significant difference between males and females at alpha = 0.05.

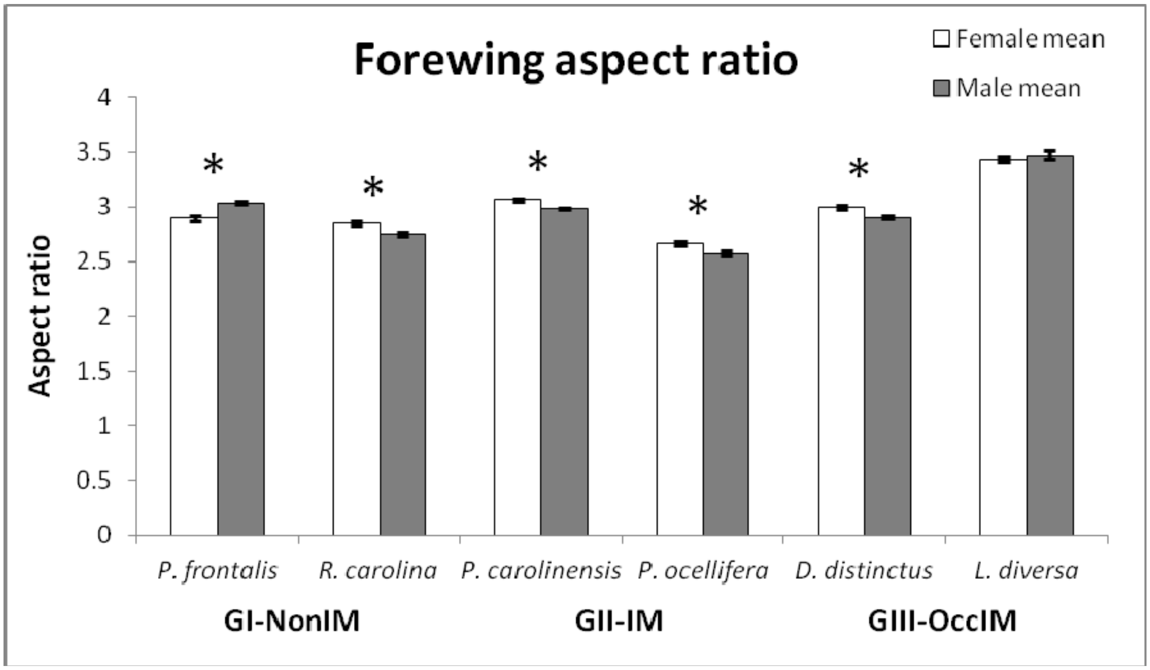


Fig. 4.2. Mean (±1 SE) forewing aspect aspect ratio for females (white) and males (grey) for each species. An asterisk represents a significant difference between males and females at alpha = 0.05.

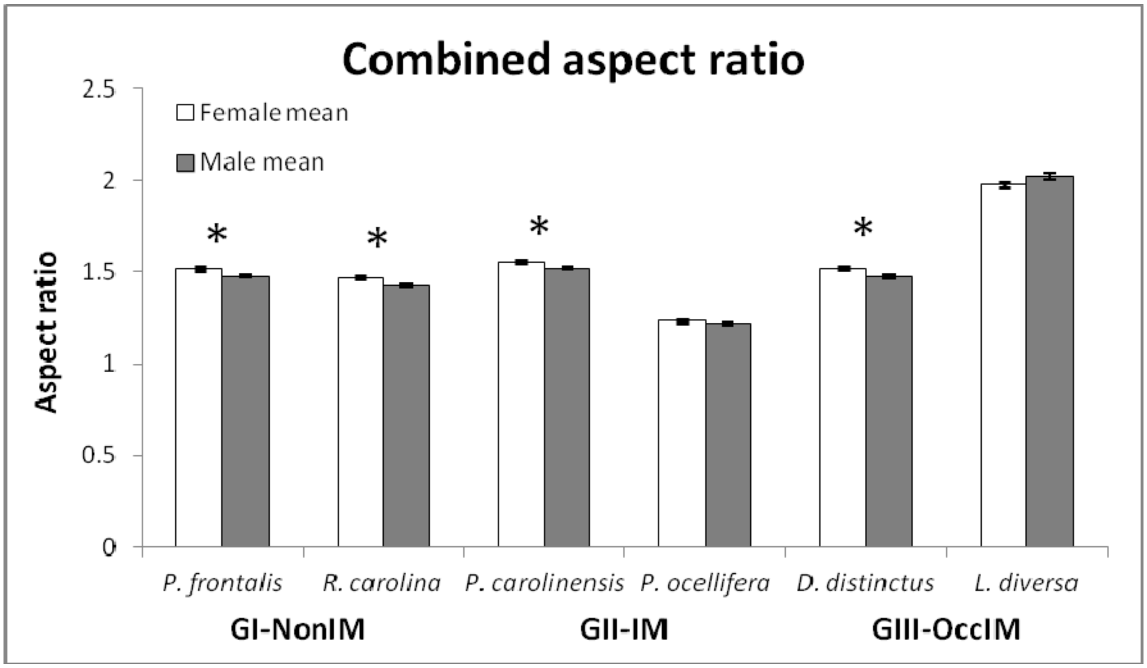


Fig. 4.3. Mean (±1 SE) combined aspect aspect ratio for females (white) and males (grey) for each species. An asterisk represents a signifnicant difference between males and females at alpha = 0.05.

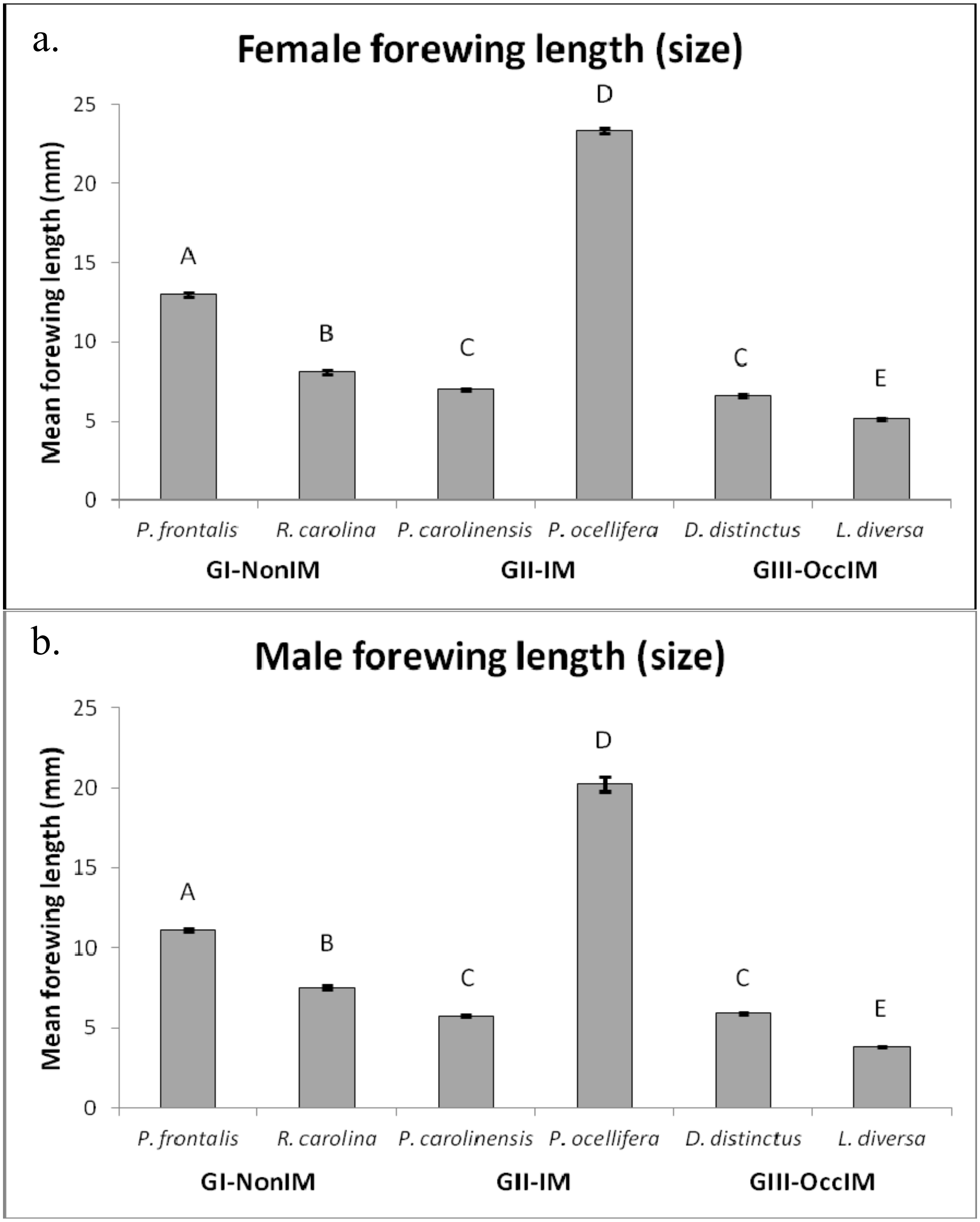


Fig. 4.4. Mean (±1 SE) forewing length (FWL) compared between species for females (a, top) and males (b, bottom). Letters represent groupings based on pairwise comparisons using Dunnett's T3 method.

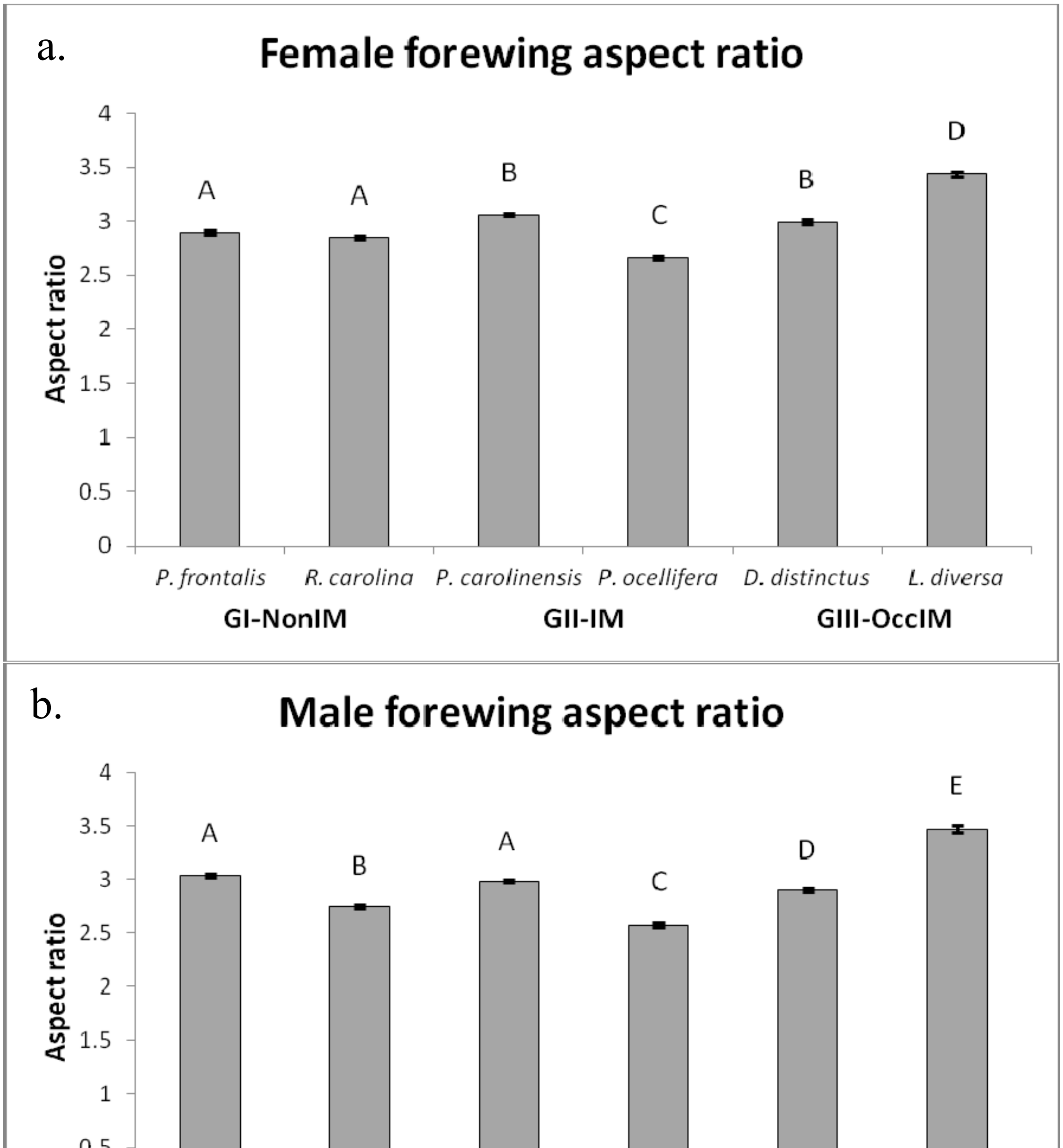


Fig. 4.5. Mean (±1 SE) forewing aspect ratio (FWAR) compared between species for females (a, top) and males (b, bottom). Letters represent groupings based on pairwise comparisons using Dunnett's T3 method.

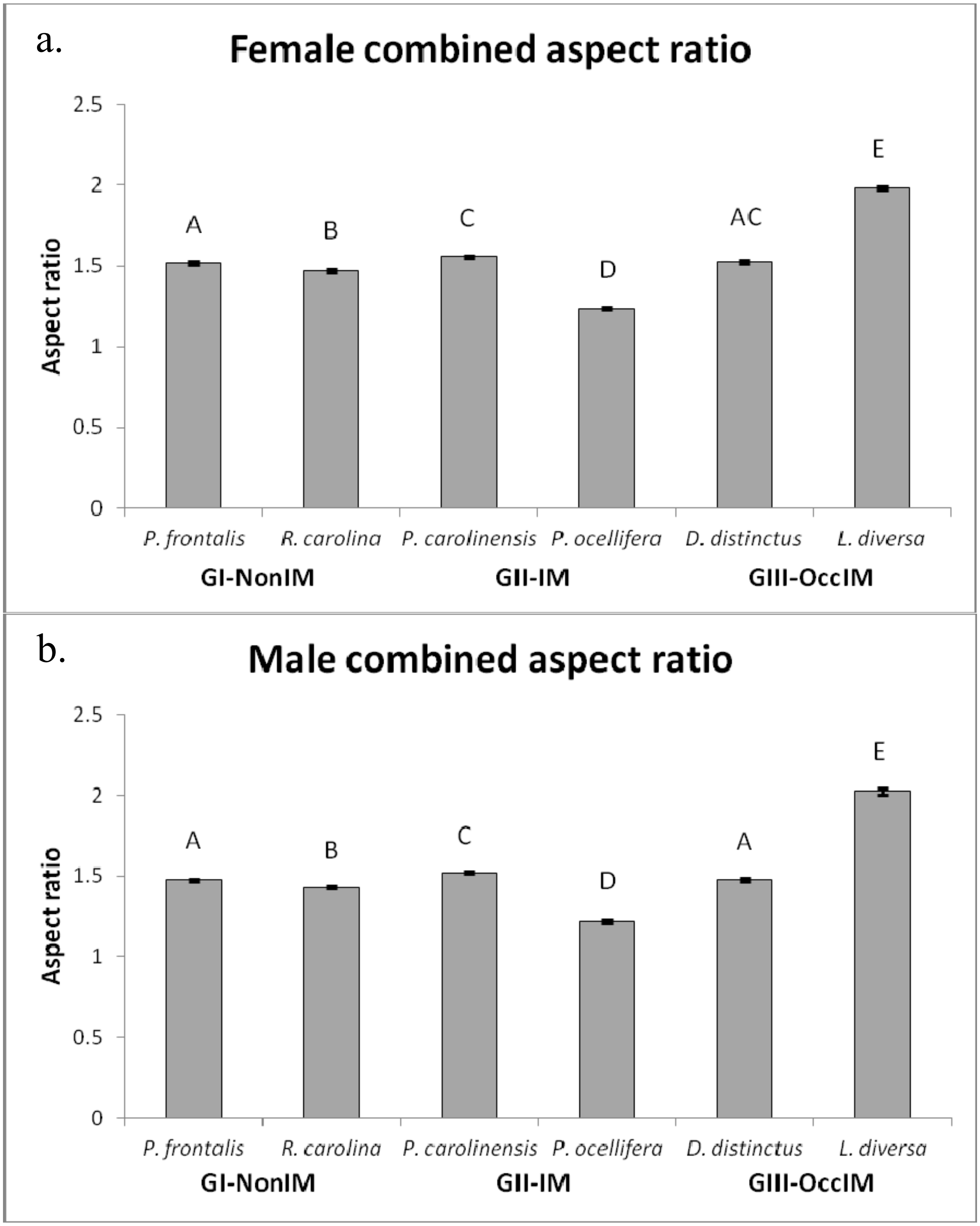


Fig. 4.6. Mean (±1 SE) fore and hindwing combined aspect ratio (CAR) compared between species for females (a, top) and males (b, bottom). Letters represent groupings based on pairwise comparisons using Dunnett's T3 method.

Discussion

Morphological features related to strong flight ability should be evident in species that readily migrate to urban streams if strong flight ability allows increased dispersal through urban landscapes. The objective of this study was to determine if wing morphological traits associated with poor flight ability were found in headwater caddisfly species that did not migrate to urban headwater streams. While differences between species were found for FWL, FWAR, and CAR, the species belonging to GI-NonIM did not have significantly lower wing lengths or wing aspect ratios. The lack of immigration to urban headwaters observed for *P. frontalis* and *R. carolina* compared to the other species did not result from inferior flight ability related to wing length or wing aspect ratio.

The morphological traits for *P. frontalis* and *R. carolina* (GI-NonIM) compared to the 4 species of immigrants (GII-IM and GIII-OccIM) provided mixes results about their flight ability. *P. frontalis* and *R. carolina* generally had long wings (only *P. ocellifera* was longer) but low wing aspect ratio (only *P. ocellifera* was lower) compared to the other taxa. Wing length is correlated with overall size in caddisflies (Petersson 1989) and is associated with greater dispersal ability. The low aspect ratio of their wings is considered aerodynamically inefficient (Vogel 1981), but limited flight efficiency could be counteracted by potentially greater energy storage resulting from the larger body size (see discussion below) (Rankin and Burchsted 1992, Elliott and Evenden 2007). Neither wing length or wing aspect ratio were substantially higher or lower respectively than the other taxa, which could indicate that a tradeoff existed between the two morphological features resulting in strong flight ability. Other morphological measures related to flight ability such as wing loading or thoracic mass may differ between these 2 species of non-immigrants (GI-NonIM) and the 4 species of immigrants (GII-IM and GIII-OccIM). In addition, the location of source populations, the location and abundance of anthropogenic features that block dispersal, and the environmental factors that decrease fitness of adults in urban landscapes (chapter 1) may have constrained movement through urban landscapes for this group independent of flight ability (Fahrig 2007). Regardless, *P. frontalis* and *R. carolina* (GI-NonIM) were not clearly strong or poor fliers compared to the other 4 taxa analyzed.

While the results failed to indicate that non-immigrants were poor flyers, two immigrants had traits that suggested they were possibly better flyers than the others. *P. ocellifera* FWL was 79.5% greater for the females and 81.3% greater for the males than *P. frontalis*, a non-immigrant (GI-NonIM), with the second longest forewings. The greater wing length matched my observation that this species had a much larger overall body size than the other species examined. *P. occellifera*, however, had the lowest FWAR and CAR for all 6 species. Its large size could indicate that potentially high energy stores allowed for long distance dispersal by this species (Rankin and Burchsted 1992, Elliott and Evenden 2007). Greater flight ability from being physically large may have outweighed the costs of an aerodynamically poor wing design for this species, and this morphological form may be suited for dispersal through urbanized landscapes. In contrast, *L. diversa* had the smallest wings but also the largest FWAR and CAR for all 6 species for both females and males. *L. diversa* CAR, which is a better measure of wing aspect ratio for this species since it employs wing coupling during flight, was 27.4% greater for the females and 33.1% greater for the males than the species with the 2nd highest CAR (*P. carolinensis*). The benefits of aerodynamically efficient wing design may have outweighed the costs of being small for this species, and allowed it to migrate through urban landscapes.

The tradeoff between size and wing aspect ratio likely occurs because of the effect of mass on maintaining flight (Hoffsten 2004). Large bodied individuals require more wing area to maintain flight (Byrne et al. 1988, Lindhe Norberg 2002), and high aspect ratio wings have less area than low aspect ratio wings for a given wing length. Thus, the trade off for having a large body size is that the species must have larger and broader wings in order to fly. An expandable area of the anal region that increased the width of the hind wing in *P. ocellifera* may be a morphological trait evolved to increase wing area.

The evolutionary bases for body size and wing aspect ratio are also dependent on adaptations to other environmental factors affecting fitness. *P. ocellifera* and *L. diversa* were found in rural headwater streams as larvae, and both species likely experienced the same selective forces for high dispersal needed for species living in unpredictable and possibly ephemeral habitats (Wilcock et al. 2007, Lowe 2009). Hoffsten (2004) found that high wing aspect ratio was related to low occupancy and poor dispersal ability for an assemblage of caddisflies and postulated that the need for maneuverability when moving through riparian vegetation or avoiding predators resulted in highly dispersive species having low wing aspect ratio (i.e., broad wings). The small size of *L. diversa* may have allowed for wind-aided dispersal (Bilton 2001). High wing aspect coupled with a small body size may be favorable for dispersing up through the canopy and entering wind currents at higher elevations. Wind-aided dispersal is a passive form of dispersal that requires less energy stores and is conducive to small body size. Further study into the relationship between flight morphology, dispersal behavior, evolutionary history, and adaptation is needed to understand how interspecific differences in flight ability impact the movement of adult stream insects through poor quality urban landscapes.

The presence of nearby source populations may have also contributed to immigration patterns for the 6 species analyzed in this study. *D. distinctus* larvae were occasionally abundant in urban headwater streams, and its immigration to other urban headwater was likely the result of its presence in nearby urban streams (Fuchs and Statzner 1990, Ahlroth et al. 2003, Sanderson 2005). The lack of a wing coupling mechanism for *D. distinctus* (Wooten 2002) suggests that it should be a poorer flier than the other 5 species. Presence in nearby urban streams could have allowed for the high levels of immigration observed in chapter 3. The immigrant species (GII-IM and GIII-OccIM) could have existed in the main-stem that each headwater flowed into. The longitudinal patterns of abundance reported in chapter 3 indicated that dispersal direction of immigrants was not consistently upstream from the confluence, and thus, not from the main-stem. Of the species belonging to GII-IM and GIII-OccIM, Smith (2006) only found larvae belonging to the genus *Dolophilodes* in the main-stem downstream of 3 of urban headwaters used to classify these taxa as immigrants. As a result, the main-stem was most likely not a significant source of adult immigrants for the GII-IM and GIII-OccIM species and a factor in their status as immigrants in this study.

Other natural factors not assessed in this study may have influenced the dispersal of these species through urban landscapes. Interspecific difference in predation rate at the source populations in rural (Paetzold and Tockner 2005) or urban landscapes

(McIntyre 2000) may have altered the abundance of immigrants from potential source populations. Interspecific differences in density dependence or reproductive behaviors that trigger dispersal (Travis et al. 1999, Bilton et al. 2001) may have also affected the patterns of immigration observed for these 6 taxa.

Measures of species traits for community ecology

Much research has focused on using species traits to predict community composition of stream fauna (Poff et al. 2006, Horrigan and Baird 2008, Statzner et al. 2008, and Verberk et al. 2008). The generation of trait matrices is often difficult and may rely on professional opinion or phylogenetic relatedness for determining a taxon's character state. The measures for each morphological trait analyzed for this study had very little variability associated with it for males and females and between species, and small numerical differences were statistically significant (Figs. 4.4, 4.5, and 4.6). Poff et al. (2006) assembled an extensive list of character traits for stream insects. They coded adult flying strength categorically as either weak or strong (i.e., binary), and only 6 of the 87 genera of caddisflies included were considered strong fliers (all Hydropsychidae) (Poff et al. 2006). Condensing this trait into 2 categories is useful for examining numerous species from several orders belonging to the entire stream insect community that incorporates many traits. The results of this study suggested that coarse trait descriptions should be avoided for studies focused on a single trait within a subset of the community such as studies investigating small differences in flight ability between species within a single order. Interspecific comparisons of traits related to flight should be done at a finer grain to encompass the small, but significant differences that may exist between taxa. More study is needed however, to determine what numerical differences in morphological traits translate into differences in flight ability that would have consequences for community dynamics. In addition, the relationships of different morphological traits to flight ability likely eliminate the use of a single continuous variable to represent flight ability, and categorical variables are likely most suited to represent flight ability. Further research is needed to expand the understanding of the trade-offs between different morphological characteristics and dispersal behavior to develop categorical representations of flight ability.

Summary

The wing morphological traits related to flight ability used in this study were poor predictors of migration by caddisflies to urban headwater streams. *P. occellifera*'s and *L. diversa*'s potentially strong flight ability may have supported the observed level of immigration to urban headwaters for these species. The physical attributes supporting strong flight differed between the species, and this difference is an example of the tradeoffs that exist between body size and wing shape for flight ability. These tradeoffs were likely the result of adaptations to the natural environment and related to dispersal behavior. The presence of local source populations of *D. distinctus* due to its larval tolerance to pollution probably resulted in the level of immigration to urban headwaters observed for this species. Flight ability is one of several factors that may determine the ability to disperse through urban landscapes, and may be the primary factor for certain species with traits supporting strong flight. While this study showed it was not the primary factor controlling immigration patterns at the assemblage level, interspecific differences in morphological traits related to flight should be considered when exploring the mechanisms controlling immigration to urban stream ecosystems.

Chapter 5: Regional and local processes structure a stream insect metacommunity existing in a partially urbanized landscape

Abstract

Metacommunity theory provides a framework for examining the importance of local and regional processes for structuring discrete communities connected through dispersal. The importance of regional versus local processes can be determined by comparing geographic distance and environmental dissimilarity to community dissimilarity among multiple communities, but patterns may be altered by landscape urbanization. I examined the relationships of geographic distance and environmental dissimilarity to community dissimilarity of a stream insect metacommunity in 4 watersheds of Maryland's Piedmont region to determine the importance of local and regional processes for structuring the metacommunity. The analysis of these relationships incorporated the effect of land use along the dispersal pathway, and the analysis compared the explanatory power of geographic distance and dispersal pathway habitat based on a Euclidean (straight line) and stream corridor dispersal pathways. Community dissimilarity was calculated for the stream insect community collected for the Maryland Department of Natural Resources, Maryland Biological Stream Survey (MBSS) monitoring program. Geographic distance and dispersal pathway habitat were determined using GIS, and environmental dissimilarity was calculated from stream habitat and chemistry variables collected for the MBSS program. Multi-model inference

testing was used to compare the explanatory power of 9 generalized linear models incorporating geographic distance, environmental dissimilarity, and/or dispersal pathway habitat for explaining community dissimilarity. The results indicated that both regional and local processes were structuring stream insect communities simultaneously. In addition, land use along the dispersal pathway improved the fit of the models, which suggested that human activities along the dispersal pathway impacted dispersal. The models incorporating the Euclidean pathway had better fit than those incorporating the corridor pathway, which supported the null hypothesis that dispersal processes affecting community composition are occurring through upland areas along a straight line between stream reaches. The results provided support for incorporating local (habitat mediated) and regional (dispersal mediated) processes into conservation and restoration strategies for lotic ecosystems in urban landscapes.

Introduction

The mechanisms that structure the composition of ecological communities can operate at different spatial scales and are dependent on dispersal, environmental conditions, and species traits (Roughgarden 1989, Poff 1997). Local scale processes refer to species interactions and species responses to habitat type and quality that occur within a specific habitat patch (Ricklefs 1987, Brown et al., 2011). Regional scale processes are based on patterns of dispersal across the landscape, which are determined by the interaction of landscape scale characteristics of habitat patches, species physical and behavioral traits related to movement, and the regional species pool (Ricklefs 1987, Roughgarden 1988, Loreau 2000, Brown et al. 2011).

The importance of regional (i.e., dispersal) and local processes (i.e., habitat suitability) for determining community composition is evident in early and contemporary ecological theories. The equilibrium theory of Island Biogeography incorporated distance (which is a determinant of dispersal) as a factor affecting colonization compared to island size (which is a descriptor of local patch habitat) as a factor affecting extinction (Morin 1999). In this model, diversity was greater for islands that were closer and larger as a result of high levels of immigration from the short distance between islands and the ability of the island to support multiple species based on its size (i.e., species-area relationships) (Morin 1999). More recently, metacommunity theory describes how regional (dispersal mediated), local (habitat mediated), and neutral processes structure communities in habitat patches through 4 perspectives: 1) patch dynamic, 2) species sorting, 3) mass effects, and 4) neutral (Leibold et al. 2004). The basic definition of a metacommunity is a set of communities inhabiting discrete habitat patches across the landscape that are connected via dispersal by organisms between patches (Leibold et al. 2004). Environmental factors at multiple spatial scales, species traits related to dispersal, and habitat requirements determine which perspective(s) best describes the process structuring the community (Cottenie 2005, Jacobson and Peres-Neto 2010). The 4 metacommunity perspectives are not mutually exclusive, and local and regional processes may act simultaneously on different subsets of the community (Chase et al. 2005, Brown et al. 2011, chapter 3).

Human activities that modify natural landscapes can alter the processes that structure metacommunities. Human activities can alter the suitability of habitat patches by altering patch size, patch shape, or environmental conditions within the habitat patch

(Picket et al. 2001). Human activities may also alter matrix habitat and eliminate habitat patches, which lead to increased fragmentation of the remaining natural habitats (Fahrig and Merriam 1994, McIntyre 2000, Elmore and Kaushal 2008). These changes may decrease survival or reproduction, constrain dispersal, and potentially alter community structure through the loss of taxa and/or the homogenization of communities across the landscape (McKinney 2002, Fahrig 2003, Fahrig 2007). While an impermeable matrix between habitat patches may decrease dispersal (Richetts 2001), habitat corridors between patches may encourage dispersal between patches, increase connectedness, and support population persistence (Fahrig and Merriam 1985).

The dendritic nature of stream ecosystems and the close connection between in-stream environments and watershed properties cause the effects of human activities on the local and regional processes controlling community structure to differ from 2-dimensional terrestrial ecosystems (Brown et al. 2011). The processes that urban land use development within the watershed alters in-stream habitat and community structure are well understood (see reviews by Paul and Meyer 2001, Walsh et al. 2005). The impact of human activities on the regional processes structuring communities depends on the mode of dispersal by different species. Taxa confined to in-stream habitat, such as fish and invertebrates incapable of flight, must disperse through the stream corridor; and as a result, dispersal is naturally constrained by the geometry of the stream network (Grant et al. 2007). Altered habitat quality in reaches of larger streams that separate headwaters may serve as a dispersal barriers to headwater taxa confined to the stream channel (Fagan 2002), and dams and culverts may block upstream migration by organisms confined to the stream channel. Organisms that can traverse the terrestrial environment, such as flight capable stream insects, are not constrained by the geometry of the stream network. The geometry of the stream network, however, does determine the landscape characteristics of stream reaches such as the distance between reaches, the amount of matrix habitat between reaches, and the spatial orientation of reaches. Interactions between the natural features of the landscape and species specific dispersal abilities and habitat preferences can determine species presence/absence (Petersen et al. 1999, Kelly et al. 2001, Finn et al. 2006, Finn et al. 2007). Land use development for human needs generally leads to lower fitness by adult stream insects, and urban landscapes may include novel barriers to dispersal that constrain movement of adults between streams (chapter 1). Any assessment of the impact of human activities on stream insect metacommunities must take into account dispersal ability and stage specific affinities for terrestrial or aquatic habitat (Jacobson and Peres-Neto 2010, Brown et al. 2011).

Alterations by land use urbanization to the local (habitat mediated) and regional (dispersal mediated) processes structuring communities may have substantial impacts on stream insects given their shifts in habitat use between developmental stages (Urban et al. 2006). Local habitat in the stream is important for the fitness of the long-lived larval stage that is highly sensitive to in-stream habitat and water quality (Walsh et al. 2005, Bonada et al. 2006). Terrestrial riparian and upland habitats surrounding the stream are important for the fitness of the adult stage (chapter 1). Adult stream insects are responsible for long distance dispersal and reproduction (Bunn and Hughes 1997, Bilton et al. 2001), and this stage most likely interacts with landscape characteristics at the regional scale. Local terrestrial habitat can effect adult survival (chapter 1), but research suggests that only a few adult individuals are needed for recruitment of the next generation of stream insect larvae (Bunn and Hughes 1997). High potential recruitment from only a few adults may limit the effect of local mortality of adults on population persistence. Chapter 3 provides evidence that urban landscapes constrain dispersal by adult caddisfly species between streams, and these constraints contributed to larval taxa loss from urban headwaters.

Relationships between geographic distance and environmental dissimilarity to community dissimilarity between pairs of adjacent communities within a large group of habitats can indicate the relative importance of local (habitat) versus regional (dispersal) processes for structuring metacommunities (Chase et al. 2005). The basis of this measurement is that communities become more dissimilar with increasing distance as dispersal between habitat patches decreases, and community dissimilarity increases as environmental dissimilarity increases due to greater habitat differences between patches (Nekola and White 1999). The strength of correlations between community dissimilarity and either geographic distance or environmental dissimilarity indicates the importance of regional versus local processes respectively.

The conclusions from distance-similarity patterns cannot be drawn using geographic distance alone in urban areas. Anthropogenic structures that prevent dispersal (chapter 1) can increase the isolation of patches independent of the actual geographic distances between patches (Fahrig 2007). As a result, geographic distance alone is not necessarily correlated to the amount of immigration occurring between 2 streams in an urban landscape. For example, two sites geographically close together may be more disconnected than two sites further apart if the land between the close sites is inhospitable.

Landscape variables that limit survival or dispersal should be factored into calculations of the effective distance between patches when testing for relationships between community dissimilarity to geographic distance and environmental dissimilarity. To accomplish this, measures of geographic distance should be modified by the characteristics of urban landscapes along potential pathways of dispersal. For stream insects, the path that adult stream insects use when migrating between reaches in adjacent watersheds is not fully resolved. Movements along the corridor (Sode and Wideberg-Larsen 1993, Petersen et al. 2004) and along a straight line through upland areas (Macneale et al. 2005) are both potential dispersal pathways for flying adult insects, and the exposure of adult insects to anthropogenic structures that constrain dispersal can differ between the two pathways. Land use development patterns in relation to the geographic position of streams may cause the types of dispersal constraints to differ between dispersal pathways, and certain anthropogenic dispersal barriers may be novel to one pathway. For example, road culverts are a potential dispersal barrier for insects flying along the stream channel (Blakely et al. 2006), but these structures are not barriers to individuals flying through upland areas.

I examined the relationships between community dissimilarity to geographic distance and environmental dissimilarity for a metacommunity of stream insects while incorporating the constraining effects on dispersal by urban land use along dispersal pathways. I hypothesized that the combination of distance between sites, dispersal pathway habitat, and environmental dissimilarity best predicted community dissimilarity between pairs of stream insect communities. To analyze these relationships, I used generalized linear models incorporating distance alone, environmental dissimilarity alone, and the combination of the 2 to explain dissimilarity between individual communities from a stream insect community data set sampled from Maryland's Piedmont region. A variable describing urban land use along the dispersal pathway was added to models that included geographic distance between sample sites. In addition, separate models that included geographic distance (and dispersal pathway habitat) were created for straight line (Euclidean) and stream corridor dispersal pathways between pairs of communities.

Methods

The overall approach was to use stream insect community and stream reach environmental data from the Maryland Department of Natural Resources (MD-DNR) Maryland Biological Stream Survey (MBSS) biomonitoring program to analyze relationships between geographic distance and environmental dissimilarity to community dissimilarity of a stream insect metacommunity. The MBSS is a stream biomonitoring program for the state of MD run by the MD-DNR that employs a "probability-based" sampling design that examines biotic and abiotic components of stream ecosystems to assess the health of Maryland's waterways (http://www.dnr.state.md.us/streams/data.asp, Klauda et al. 1998). Geographic coordinates of MBSS sample site locations and available GIS data on stream locations in MD (see details below) were used to calculate geographic distance along the stream corridor and along a straight line (i.e., Euclidean distance) between sample site pairs. MBSS data was used to calculate 1) environmental dissimilarity between sample sites based on available habitat and stream chemistry data and 2) stream insect community dissimilarity between sample sites. Variables representing the land use along each dispersal pathway were calculated from publically available land use data using GIS analysis (see details below). The power of geographic distance, environmental dissimilarity, and/or dispersal pathway habitat for explaining patterns of community dissimilarity between sites was determined using multimodel inference testing.

Site selection

Geographic location, available habitat data, and available benthic community data were used as the basis for selecting sites from rounds 2 and 3 (years 2000 to 2009) of the MD-DNR MBSS dataset for inclusion in this study. The data included for analysis was only from Maryland's Piedmont physiographic province to minimize the effect of habitat and community differences that typically occur naturally and as a result of human impacts in different physiographic provinces (Morgan and Cushman 2005, Utz et al. 2009). Geographic coordinates of sample sites were imported into ArcMAP v10.1 (Esri, Redlands, CA) and compared to the geographic locations of streams in the USGS National Hydrology Dataset (NHD), Flowline data for stream channels (flowline). Sample site locations were moved to the closest flowline location using ArcMAP (*NearXY* tool). These repositioned sample site locations were visually compared to the original locations to ensure that sites were relocated to appropriate locations along the flowlines. The representation of large rivers as line data by the flowlines occasionally caused sample sites along large rivers to relocate to flowlines for tributaries entering the rivers. A GIS layer of water body boundaries from the Maryland State Highway Administration (MD-SHA) and the site names listed in the MBSS data set were used to help identify locations where sample sites of large rivers were incorrectly moved to tributaries, and the correct location was noted for further analysis (note: as described below, sample site locations along large rivers were removed from the analysis).

Sample site locations along flowlines were visually inspected within ArcMAP v10.1 to determine stream order (1^{st}, 2^{nd}, or $\geq 3^{rd}$) and if any sampling sites occurred upstream of the sample site location. Only those sample sites on 1^{st} and 2^{nd} order streams and without any sample sites upstream were retained for analysis (i.e., larger river sites were eliminated in this step). Stream reaches along the same branch that are located up or downstream of each other likely have similar communities from spatial autocorrelation and from the process of downstream drift of individuals (Heino et al. 2005), and this level of spatial autocorrelation was not the focus of this study.

An *a priori* decision was made that comparisons of geographic distance and environmental dissimilarity to community dissimilarity between communities separated along the river network by the Chesapeake Bay would not provide meaningful information about the importance of the Euclidean versus corridor dispersal pathways for determining community similarity. As a result, comparisons of community similarity were only performed for communities located within the Piedmont of the Bush, Gunpowder, Patapsco, Patuxent, and Susquehanna (Maryland Department of the Environment 6 digit – MDE6) watersheds individually. Any sample site not from these watersheds was removed. Any subset of sample sites within these watersheds that was separated along the stream corridor from the majority of sample sites by the Chesapeake Bay was eliminated as well. Additional sample sites were removed from the analysis based on the availability of habitat and benthic invertebrate data (See below). The final analysis included 189 MBSS sample sites across all 5 MDE6 watersheds, which resulted in a total of 4,157 sample site pairs (Table 5.1). Each sample site pair was a replicate in the analysis comparing geographic distance and environmental dissimilarity to community dissimilarity.

Table 5.1. List of MDE6 watersheds examined in this study, the total number of MBSS sample sites from each watershed, and the resulting number of stream pairs, which represents the number of replicates used in the analysis.

MDE6 watershed	Total sample sites	Pairs of sites analyzed
Bush	17	136
Gunpowder	51	1275
Patapsco	58	1653
Patuxent	20	190
Susquehanna	43	903
Total	***189***	***4157***

Geographic distance and dispersal pathway habitat

Two sets of dispersal pathways between sample site locations were created using ArcMAP v10.1 (*XY to line* and *Network Analyst* tools). The Euclidean pathway was created as a geodesic line following a direct route between all pairs of sites within each MDE6 watershed. The stream corridor pathway was created as a geodesic line following stream flowlines between each pair of sample sites within each MDE6 watershed. Total distance in kilometers between each sample site pair was determined for both types of dispersal pathways, and this value was used as the geographic distance in the model selection procedure.

Buffers around each dispersal pathway created using ArcMAP v10.1 (*Buffer* tool) were used to characterize land use along each corridor and Euclidean dispersal pathway. A 100m buffer was created along each Euclidean pathway, and 30m and 100m buffers were created along each corridor pathway. Terrestrial habitat variables listed in Table 5.2 were calculated for the appropriate buffer for each dispersal pathway. Forested, commercial, and high density residential land-covers were calculated from 2010 Maryland Department of Planning (MDP) land-cover / land use data. Impervious surfaces were calculated from United States Geological Survey (USGS) National Land Cover Database 2006 impervious surface estimate data. Percent impervious surface was used to represent temperature increases in urban areas. Greater impervious surfaces are related to greater land (Yuan and Bauer 2007) and air (Myint et al. 2010) temperatures, and air temperature data was not available at the grain size required for this analysis. Road locations data was from Maryland State Highway Administration (MD-SHA) Centerline NAD83m road data. The community data used was collected between 2000 and 2009 during which time land use affecting dispersal could have changed. The data used in this study represented the data sources available with the greatest temporal overlap with the community data. MDP 2010 land use data was constructed from a land use database released in 2002 and updated with data collected prior to 2008 (see MDP land-cover / land use metadata, http://www.mdp.state.md.us/PDF/OurWork/LandUse/metadata.pdf).

Buffer size used for individual variables was based on an estimated spatial scale of effect on adult stream insects. The effects of impervious surfaces on temperature and commercial and high density residential land use on artificial light were expected to extend outward from the locations where both geographically occurred in the landscape (Pickett et al. 2001, Eisenbeis 2006). As a result, both variables were measured within a 100m buffer to capture the extended scale of impact along each dispersal route. Empirical evidence suggests that if stream insects disperse along the stream corridor they stay close to the stream channel (Petersen et al. 1999). Percent forested land use was measured within a smaller 30m buffer along the corridor dispersal pathways. A similar assumption could not be made for individuals moving along the Euclidean pathway, and percent forested area was measured within a larger 100m buffer to gauge the general trend in this land use variable between sample site pairs.

The GIS analysis of land use along the dispersal pathways resulted in 4 individual measures of dispersal pathway habitat between each sample site pair for Euclidean and corridor dispersal pathways (Table 5.2). An aggregate measure of the land use representing the potential dispersal constraints occurring along each type of dispersal pathway was created for the model selection procedure using Principle Components Analysis (PCA). A PCA using the variance/covariance matrix was performed using R v2.14.1 (*princomp* protocol; *stats* package 2011) to reduce the 4 variables for each dispersal pathway into a single variable representing an aggregate description of land-use along the dispersal pathway. The first principle component (PC) from the PCA was retained and used as a single explanatory variable representing the 4 land use variables for each sample site pair. The first PC is an orthogonal variable representing multiple response variables. Given the high amount of variance explained by this variable (see below), I decided it was sufficient to summarize dispersal pathway habitat between sample site pairs. The PCA was run on land use variables for all sample site pairs together rather than individually within each watershed. Running the PCA for all sample site pairs was done to keep the variance explained by this variable equal across all watersheds for the model selection process.

Stream insect community data and community dissimilarity

Field collections of the benthic community by the MD-DNR were done using the standard MBSS protocols described by Stranko et al. (2007). In summary, sampling was done along a 75m reach from multiple habitats using a D-framed net. Riffle habitats were sampled by disturbing benthic substrate by hand or foot and allowing sample debris to be carried by the current downstream into the D-net. Large substrates such as logs and snags were sampled in a similar fashion but only by hand. All other habitats were sampled by jabbing at or sweeping through them with the D-net to collect benthic invertebrates. Specimens were preserved in 95% ethanol in the field and returned to the lab for processing and identification.

Sample processing and identification were done using the standard MBSS protocols described by Boward and Friedman (2011). A 100 specimen subsample of benthic invertebrates was removed from the sample debris. Specimens were identified to genus when possible using dissecting microscopes, but family and order level identifications occurred as well. Thus, benthic invertebrate data included specimens identified to family or order that may actually represent genera assigned to other specimens in the same or other samples.

Table 5.2. List of landscape variables that may impact dispersal. These variables were included in the PCA to create a single variable (from the first PC) representing dispersal pathway habitat between each sample site pair. The summary variable based on the first PC was included in the model selection process.

Landscape scale variables	Potential impact to dispersal[a]	Measure for Euclidean pathway	Measure for corridor pathway
Forested area along dispersal pathway	Forested areas encourages dispersal (Petersen et al. 1999)	Percent forested area in 100m buffer	Percent forested area in 30m buffer
Road – stream intersections (bridges and culverts)	Bridges and culverts are a barrier to dispersal (Blakely et al. 2006)	Not applicable	Total number of stream-road intersections per km
Temperature on land	High temperatures decrease adult stream insect survival, may discourage dispersal (Collier and Smith 2000)	Percent impervious surfaces in 100m buffer	Percent impervious surfaces in 100m buffer
Paved surfaces (roads)	Possible environmental sink, may discourage dispersal (Kriska et al. 1998)	Number of road-dispersal pathway intersections per km	Not applicable
Artificial light sources	Possible environmental sink, may discourage dispersal (Perkin et al. 2011)	Percent commercial and high density residential land use in 100m buffer	Percent commercial and high density residential land use in 100m buffer

[a] See chapter 1 for full description of potential impacts to adults

All non-Insecta were removed from the dataset as well as those coded as Collembola (n = 6), Isotomidae (Collembola) (n = 2), *Isotomurus* (Collembola: Isotomidae) (n = 5), Lepidoptera (n = 3), and Curculionidae (n = 1). All Collembola were removed due to their lack of a flight capable stage. All Lepidoptera identified to order were removed because all fully aquatic lepidopteran larvae are generally easily identified to at least family given the presence of conspicuous gill structures along their abdomen, and as a result, those identified to order were considered accidentally collected terrestrial taxa. Aquatic Curculionidae do not differ significantly from terrestrial Curculionidae, and all Curculionidae taxa were removed because specimens included in the MBSS dataset may actually be terrestrial taxa collected accidentally. The specimens from these taxa represented a very small portion of the entire data set (0.086% of all specimens included).

Taxonomic resolution used for specimen identifications between sample sites must be equal to effectively measure dissimilarity between communities (Cao and Hawkins 2011). For example, communities may appear more dissimilar if a specimen of Genus A is identified to the family level at some sites and to the genus level (i.e., Genus A) at other sites. The lack of consistent taxonomic resolution across specimens to the MBSS dataset required alterations to taxonomic designations or the deletion of taxa from the dataset (Cao and Hawkins 2011). The subset of specimens identified to family (or order) were removed from the analysis or all specimens with genus level identifications were changed to a family level designation (i.e., the taxonomic resolution was scaled up from genus) when multiple levels of taxonomy were assigned to individuals belonging to a single family. The specimens identified to genus were changed to family if the arbitrary statistic:

$$x = 10 * (\text{no. family} / \text{total abundance})$$

where no. family = the abundance of all specimens identified to family from all samples and total abundance = the total abundance of all specimens from the family regardless of taxonomic designation, was greater than the number of genera recorded for the family being evaluated. Specimens with family level identifications were removed from the data set if x was lower than the number of genera recorded for the family being evaluated. For example, if 50 specimens were identified to family out of 100 total specimens from that family ($x = 10*50/100 = 5$) and only 3 genera were identified, then all specimens identified to genus were reclassified at the family level ($x > 3$). If 20 specimens were identified to family out of 100 total specimens from that family ($x = 10*20/100 = 2$) and 5 genera were identified from that family, then the specimens identified to family were deleted from the data set ($x < 5$). This statistic was contrived specifically for this study, and it was designed so that specimens identified to genus were changed to a family level designation if a large portion of all individuals were identified to family. Specimens identified to family or order were deleted when family level identifications represented a small portion of the overall number of specimens identified for a family. This procedure minimized the amount of community data lost and resulted in 19,821 individuals from 193 taxonomic units used in the analysis of community dissimilarity.

The Jaccard index of dissimilarity:

$$C_J = (A+B-2*J)/(A+B-J)$$

where A = number of taxa at sample site A, B = the number of taxa at sample site B, and J = the number of taxa shared by samples sites A and B, was calculated for the stream insect communities from the sample site pairs for each MDE6 watershed. Pairs of sample sites that shared no taxa had a dissimilarity value of 1, and pairs of sites that shared all taxa have a dissimilarity value of 0. Measures of Jaccard dissimilarity were calculated from presence/absence data using R v2.14.1 (*vegdist* protocol; *vegan* package v2.0-2). Alterations to the data based on issues with taxonomic resolution, the deletion of non-insect and other select taxa, and the fact that MBSS samples are 100 specimen subsamples made comparisons of abundance between sample sites unreliable; and as a result, dissimilarity was calculated based on presence/absence data.

Environmental dissimilarity

Habitat data used for describing environmental dissimilarity between sample sites came from MBSS habitat and stream chemistry data. Habitat and chemistry data were collected using the standard MBSS protocols describe by Stranko et al. 2007. In summary, 17 stream chemistry measurements were made either in the field or laboratory. Conductivity and pH were measured in the field and in the lab, and all other variables were measured using only one method. Grab samples for water chemistry analysis and field measurements were done at the top of the sampling reach where stream invertebrate samples were collected. Ten habitat variables were also measured at each sampling location. These measures included qualitative assessment of in-stream habitat and riparian condition and quantitative measures of average stream width (m), average thalweg depth (cm), average velocity (m/s), and maximum depth (cm). The average for each quantitative variable was calculated from measures at 4 evenly spaced transects along the 75m reach (0m, 25m, 50m, and 75m), and maximum depth was a single measurement from within the reach.

A subset of the chemistry and habitat variables were used to define environmental similarity between sample sites for this study. Nutrient concentrations (e.g., nitrogen and phosphorus) are important predictors of overall water quality and are often correlated to urban land use (Roy et al. 2003), but direct effects of elevated nutrient concentrations on insect fitness in the stream are difficult to discern given the number of confounding factors and interactions that can occur in urban stream environments (Yuan 2010). Conductivity is also a chemical parameter that typically shows a high correlation with human impacts to streams and overall stream quality and is consistently correlated with changes in the composition of stream insect communities along a gradient of stream quality (Roy et al. 2003). As a result, conductivity (μ-mohs/cm, field measure) was included in the analysis to serve as an indirect measure of overall habitat and stream quality. Dissolved oxygen (mg/L, field measure), pH (field measure), and turbulence (NTU, field measure) were the only chemical variables measured that directly described aspects of larval insect habitat, and these variables were included in the analysis. The greater number of missing data points for laboratory than field measurements for conductivity and pH and several potential outliers identified in the laboratory measurements for conductivity resulted in the use of field measurements for these variables in the analysis. All quantitative measures of stream habitat except maximum stream depth and all qualitative measures of habitat quality (e.g., in-stream habitat, epifaunal substrate, velocity depth diversity, pool quality, riffle quality, percent embedded, and percent shading by the riparian vegetation) were included in the analysis.

Descriptions of these variables are provided by Stranko et al. (2007). A lack of data at certain sample sites for the variables selected also resulted in the elimination of suitable sample sites from the analysis.

A PCA using the correlation matrix was performed on the environmental variables across all sites to calculate environmental dissimilarity between sample site pairs (R v2.14.1; *princomp* protocol; *stats* package 2011). Using the correlation matrix standardizes the variances of all variables to 1 and allows all variables to contribute equally to each PC. All PC's with an eigenvalue >1 were retained based on the Kaiser-Guttman criterion (Legendre and Legendre 1998). The scores corresponding to each sample site location from each retained PC identified the location of the sample in ordination space, and these values were used to calculate Euclidean distance between sites using R v2.14.1 (*dist* protocol; *stats* package 2011). Distance in ordination space represents the dissimilarity of the environmental measurements between site pairs (e.g., large distances indicated dissimilarity). Thus, Euclidean distance was a single value representing the environmental dissimilarity between all pairs of sites. The PCA was run on the entire data set to ensure that variability criteria used to select individual PC's was the same across samples when analyzed simultaneously during the model selection procedure (not within each MDE6 watersheds). Calculation of Euclidean distance for environmental variables between sites was only performed between sample site pairs within MDE6 watersheds since the model selection procedure was only done with variables calculated between samples sites within each watershed.

Model selection

Multimodel inference was used to determine the importance of geographic distance, dispersal pathway habitat, and environmental dissimilarity for explaining patterns of community dissimilarity between sites (Anderson 2008). The theory behind this method is that statistical models relating independent and dependent variables representing specific competing hypotheses are developed *a priori*, and the fit of each model to the available data is tested to determine which hypothesis has the most support from the available data. Akiake's information criterion (AIC) or second-order AIC (AICc) values are calculated for each model and indicate model support. The model with the lowest (possibly most negative) AIC/AICc value is considered the best model of those proposed, and the hypothesis related to that model is considered the accepted hypothesis based on the available data.

For this analysis, models were developed that used 1) geographic distance only, 2) environmental dissimilarity only, 3) a combination of geographic distance and dispersal pathway habitat, 4) a combination of geographic distance and environmental dissimilarity, and 5) a combination of geographic distance, dispersal pathway habitat, and environmental dissimilarity (Table 5.3). Separate models were included for Euclidean and corridor pathways whenever geographic distance was included in the model. Correlation between Euclidean and corridor dispersal pathway distances likely occur given that sample site pairs included in the analysis were restricted to those within MDE6 watersheds. Both variables did not occur within a single model and any correlation would not have affected model fit statistics for individual models. However, differences in fit between models that incorporate each type of geographic distance may be impacted by correlations between Euclidean and corridor dispersal pathway distances. The Pearson's correlation coefficient was calculated to test for this correlation. The entire set of models based on all potential combinations of explanatory variables and the global model were not analyzed since many models, including the global model, did not represent hypotheses of interest. For example, a model using Euclidean distance and corridor dispersal pathway habitat does not represent a legitimate hypothesis for what is controlling community dissimilarity between sample site pairs.

Generalized linear models with only additive terms were created using the explanatory variables, and AICc scores were generated using R v2.14.1 (*glm* protocol; *stats* package 2011, and *AICc.glm* protocol; *AICcmodavg* package v1.24 respectively). The model was run using variables calculated for all sample site pairs within each watershed without regard for which MDE6 watershed the sample site pairs belonged to. AICc values were compared between models, and the model with the lowest value was considered the model with the best support. Support for a single best model was assessed by comparing Δ_i ($AICc_i$-$AICc_{min}$), which represents the difference in AICc values between each model and the best model. Adjusted R^2 was calculated from a linear model formula for each model (R v2.14.1; *lm* protocol; *stats* package 2011) to determine how much of the variance in community dissimilarity was explained by each model. The log likelihood of each model was calculated using R v2.14.1 (*logLik* protocol; *stats* package 2011) and used as another measure of support for the models. Variance inflation factors for models 8 and 9, which included the most parameters, were calculated using R v2.14.1 (*vif* protocol; *car* package 2011) to check for overdispersion, which indicates potential problems with a lack of independence and/or heterogeneous distributions between variables (Anderson 2008). In addition, Pearson's correlation coefficient was calculated between each geographic distance (Euclidean and corridor) and environmental dissimilarity. The correlation analysis with these variables was done specifically to determine if environmental similarity is dependent on the distance between sample sites (i.e., spatial autocorrelation).

Results

Geographic distances and dispersal pathway habitat

Euclidean pathway distances were shorter than corridor pathway distances since elevation was not included when calculating distance (Table 5.4). Euclidean pathway distances between sample sites ranged from 0.5 to 54.4km with an average distance across all sample site pairs of 18.6km. Corridor pathway distances ranged from 0.8 to 140km with an average distance across all sample site pairs of 53.44km. The Pearson's correlation coefficient calculated for Euclidean and corridor dispersal pathway distances was 0.59 which indicated a moderately high amount of correlation between these variables.

(Table 5.3 - Caption)

Table 5.3. List of models including model structure, description of the local or regional process the corresponding hypotheses support, and the results of the model selection procedure. Structure, description, and results for the best model are in bold.

(Table 5.3 - illustration)

Model structure[a]	Processes supported	AICc score	Rank[b]	Δ_i[c]	adj. R^2 [d]	LL[e]
$C_J = D_{euc}$	Regional (Euclidean dispersal pathway)	-8263.558	7	450.309	0.0405	4134.782
$C_J = D_{cor}$	Regional (corridor dispersal pathway)	-8155.398	9	558.469	0.0152	4080.702
$C_J = E$	Local	-8483.993	5	229.874	0.0901	4244.999
$C_J = D_{euc} + B_{euc}$	Regional (Euclidean dispersal pathway, dispersal impacted by land use)	-8453.783	6	260.084	0.0836	4230.896
$C_J = D_{cor} + B_{cor}$	Regional (Corridor dispersal pathway, dispersal impacted by land use)	-8165.702	8	548.165	0.0179	4086.856
$C_J = D_{euc} + E$	Regional (Euclidean dispersal pathway) & local	-8611.822	2	102.045	0.1178	4309.916
$C_J = D_{cor} + E$	Regional (corridor dispersal pathway) & local	-8523.003	4	190.864	0.0988	4265.506
$C_J = D_{euc} + B_{euc} + E$	Regional (Euclidean dispersal pathway, dispersal impacted by land use) & local	**-8713.867**	**1**	**0**	**0.1394**	**4361.941**
$C_J = D_{cor} + B_{cor} + E$	Regional (Corridor dispersal pathway, dispersal impacted by land use) & local	-8530.936	3	182.931	0.1007	4270.475

[a] The variables in the models are: J = Jaccard dissimilarity index, D_{euc} = Euclidean geographic distance, D_{cor} = corridor geographic distance, E = environmental dissimilarity between sample site pairs, B_{euc} = Euclidean dispersal pathway habitat, B_{cor} = corridor dispersal pathway habitat

[b] Models are ranked 1 to 9 from the lowest AICc score (signifying the best model) to highest AICc scores

[c] Δ_i represents the difference between AICc scores for each model and the best model

[d] The adjusted R^2 was calculated using a linear model formula

[e] Log likelihood

Table 5.4. Summary of geographic distances between sample site pairs and dispersal pathway variables used in the PCA to calculate the dispersal pathway habitat variable used in the model selection procedure.

	Euclidean dispersal pathway														
	Distance (km)			% Forested[a]			% Impervious[b]			% Com/hd-res[c]			Road int. (no./km)[d]		
Watershed	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Bush	0.8	9.3	22.7	1.0	23.0	51.3	5.5	49.2	90.3	0.0	9.8	41.5	0.00	3.31	6.48
Gunpowder	0.9	21.4	53.2	0.1	32.7	89.4	0.2	18.5	94.2	0.0	2.0	48.8	0.00	1.39	8.01
Patapsco	0.9	18.8	54.4	0.0	30.5	99.5	0.0	31.1	93.5	0.0	6.8	48.0	0.00	1.98	11.20
Patuxent	0.8	13.9	33.2	6.7	27.7	59.3	1.9	17.8	71.9	0.0	1.0	14.6	0.36	1.41	4.60
Susquehanna	0.5	17.0	43.3	1.6	30.4	75.8	0.7	8.8	35.8	0.0	0.5	11.7	0.00	0.99	2.39
	Corridor dispersal pathway														
	Distance (km)			% Forested[e]			% Impervious[b]			% Com/hd-res[c]			Road int. (no./km)[d]		
Watershed	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Bush	2.3	26.8	64.8	9.1	50.2	81.2	4.4	20.6	66.0	0.0	4.3	17.7	0.00	0.66	1.58
Gunpowder	1.3	55.3	127.1	6.1	59.4	97.4	0.4	7.4	57.0	0.0	0.4	13.4	0.00	0.48	2.42
Patapsco	1.5	59.0	132.4	7.8	57.7	100.0	0.0	17.4	63.1	0.0	2.1	24.8	0.00	0.51	2.42
Patuxent	5.6	69.9	140.0	23.7	73.4	95.0	2.0	9.6	33.7	0.0	1.9	11.8	0.13	0.47	1.20
Susquehanna	0.8	41.3	107.2	0.0	52.8	99.0	0.9	7.8	19.4	0.0	0.1	2.6	0.00	0.35	1.00

[a] % Forested is the percent forested land use was calculated for a 100m buffer around the dispersal pathway

[b] % Impervious is the percent impervious surfaces calculated for a 100m buffer around the dispersal pathway

[c] % Com/hd-res is the percent commercial and high density residential land use in a 100m buffer around the dispersal pathway

[d] Road int. is the number of road-dispersal pathway interactions per km

[e] % Forested is the percent forested land use calculated for a 30m buffer around the dispersal pathway

Euclidean dispersal pathway habitats differed between MDE6 watersheds (Table 5.4). Percent forested land use in the 100m buffer had a maximum value of 99.5% and a minimum value of 0% across all watersheds. Minimum values for percent forest were generally low across all watersheds with the greatest minimum being 6.7% in the Patuxent watershed. Maximum values for percent forest varied from 51.3% within the Bush watershed to 99.5% within the Patapsco watershed. Percent impervious surfaces within the 100m buffer showed a similar pattern. The Susquehanna dispersal pathways had a maximum percent impervious of 35.8% while the Patuxent watershed had a maximum of 71.9%. The other three watersheds had maxima greater than 90%. Minimum percent imperviousness were all generally low with the greatest minimum of 5.5% being found in the Bush watershed. Average percent imperviousness in the 100m buffer ranged from 8.9% to 49.2% across all watersheds. Percent commercial and high density residential land use in 100m buffers had minimums of 0% at all watersheds, and the maxima varied from 11.7% to 48.8%. Average percent commercial and high density residential land use was generally low and varied from 0.5% to 9.8%. Road-dispersal pathway intersections varied from a minimum of 0 to a maximum of 11.2 intersections/km. The average intersections ranged from 0.99 to 3.31 intersections/km between watersheds.

Corridor dispersal pathway also differed between MDE6 watersheds (Table 5.4). Percent forested land use in the 30m buffer had a maximum value of 100% and was no lower than 81.2% (Bush watershed). Average percent forested land use ranged from 50.2% to 73.4% across all watersheds. Percent impervious surfaces in the 100m buffer showed a similar pattern to the Euclidean dispersal pathways. The Susquehanna sample sites also had the lowest maximum percent imperviousness of 19.4%, while the other watersheds had maxima that ranged between 33.7% and 66%. Minimum percent imperviousness were all generally low with the greatest minimum of 4.4% also being found in the Bush watershed. Average percent imperviousness ranged from 7.4% to 20.6% across all watersheds. Percent commercial and high density residential land use in the 100m buffer had minimums of 0% at all watersheds, and maxima varied from 2.6% to 24.8%. Average percent commercial and high-density residential land use were generally low and varied from 0.1% to 4.3%. Road-dispersal pathway intersections varied from a minimum of 0 to a maximum of 2.42 intersections/km. Average intersections ranged from 0.35 to 0.66 intersections/km across all watersheds.

The PCA performed on the Euclidean dispersal pathways resulted in PC1 with an eigenvalue of 380.02, which accounted for 75.3% of the variance. Factor loadings for PC1 were greatest for percent impervious surfaces in the 100m buffer (-0.899) and percent forest in the 100m buffer (0.345). The factor loadings indicated that PC1 scores were negatively related to the percent impervious surfaces in the 100m buffer, and less related positively to percent forested area in the 100m buffer.

The PCA performed on the corridor dispersal pathway resulted in PC1 with an eigenvalue of 233.16, which accounted for 71.3% of the variance. Percent forested area in the 30m buffer had the highest factor loading for PC1 (0.999). The factor loadings indicated that PC1 scores were highly positively related to the percent forested land use in the in the 30m buffer.

Environmental dissimilarity

Drastic differences for environmental variables between MDE6 watersheds were generally uncommon (Table 5.5). Average conductivity ranged from 189.1 to 323.1 µ-mohs/cm across all watersheds. However, the greatest maximum conductivity measured at any watershed was 1,330 µ-mohs/cm within the Patapsco watershed while the smallest maximum measured was 540 µ-mohs/cm within the Patuxent watershed. Mean turbidity for the Bush watershed (10.2 NTU) was twice as large as the means in the Patapsco, Patuxent, and Susquehanna watersheds. Mean percent stream shading varied relatively little across watersheds (range from 77.3% to 86.2%), but the ranges differed across watersheds. Maximum percent shading ranged from 95% to 99% across all watersheds, but minimum values ranged from 5% to 60%.

The PCA of environmental variables resulted in 4 PC's having eigenvalues greater than 1 being retained (Legendre and Legendre 1998) for calculations of environmental dissimilarity (Table 5.6). PC1 was associated with 34.8% of the standardized variance in the dataset and was most related negatively to in-stream habitat (factor loading = -0.400). PC's 1 through 4 were associated with 74.6% of the total variance in the environmental data. The eigenvalues and greatest factor loadings for each retained PC are listed in Table 5.6.

(Table 5.5 - caption)

Table 5.5. Summary of environmental variables used to calculate environmental dissimilarity. Listed are the minimum, mean, and maximum values for each watershed for each variable.

(Table 5.5 – illustration)

	Chemistry											
	DO[a] (mg/L)			pH			Cond[b] (μ-mohs/cm)			Turbidity (NTU)		
Watershed	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Bush	6.2	8.1	10.3	6.4	7.0	7.9	164	323.1	628	1.1	10.2	58.2
Gunpowder	4.8	8.1	9.7	6.3	7.3	7.9	90	244.3	1000	0.1	7.4	222
Patapsco	3.3	8.3	17.9	5.2	7.3	9.1	100	331.3	1330	0.1	4.3	22.3
Patuxent	3.7	7.5	9.1	6.5	6.9	7.7	80	200.6	540	0.7	5.6	14.9
Susquehanna	4.7	8.6	11.6	6.2	7.0	8.5	89	189.1	851	0.3	4.4	35.8

	Stream habitat														
	In-stream habitat			Epi substrate[c]			Vel-depth[d] diversity			Pool quality			Riffle quality		
Watershed	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Bush	2	11.8	16	1	11.4	16	2	9.647	15	6	11.2	16	2	8.7	2
Gunpowder	3	12.5	18	3	12.4	19	4	9.431	15	3	9.9	17	0	11.0	0
Patapsco	1	12.9	18	2	13.3	18	1	9.155	16	3	9.5	16	0	11.1	0
Patuxent	1	12.1	17	1	12.0	17	2	10.05	14	1	10.3	18	1	11.0	1
Susquehanna	6	12.7	17	4	13.2	18	6	10.19	17	4	10.1	16	4	12.3	4

	Physical characteristics														
	Percent embedded			Percent shading			Ave width[e] (m)			Ave depth[f] (cm)			Ave velocity (m/s)		
Watershed	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Bush	0	29.88	70	15.0	81.6	95.0	0.52	2.6	6.18	5.25	19.2	48.25	0.01	0.11	0.28
Gunpowder	9	37.49	95	5.0	77.3	98.0	0.42	2.3	7.50	5.00	17.4	58.75	0.01	0.17	0.63
Patapsco	0	33.59	100	12.0	83.1	99.0	0.65	2.7	7.85	3.50	15.7	44.50	0.00	0.17	0.49
Patuxent	15	35.75	100	60.0	86.2	95.0	0.32	2.3	4.60	3.25	16.5	36.50	0.01	0.10	0.25
Susquehanna	5	26.88	100	30.0	81.3	99.0	0.68	2.7	5.85	5.00	19.8	37.50	0.02	0.20	0.80

[a] DO = dissolved oxygen

[b] Cond = conductivity

[c] Epi substrate = epifaunal substrate

[d] Vel-depth = velocity depth

[e] Ave width = average stream width

[f] Ave depth = average depth in thalweg

Table 5.6. Results of the PCA on chemistry and habitat variables for calculating environmental dissimilarity between sample site pairs.

PC	Eigenvalue	% Variance Explained	Retained[a]	Factor (loading)
1	4.871	34.8%	Yes	In-stream habitat (-0.400)
2	1.913	13.7%	Yes	Ave depth (0.421)
3	1.475	10.5%	Yes	DO (0.564)
4	1.345	9.6%	Yes	pH (0.528)
5	0.955	6.8%	No	NA
6	0.801	5.7%	No	NA
7	0.682	4.9%	No	NA
8	0.505	3.6%	No	NA
9	0.477	3.4%	No	NA
10	0.321	2.3%	No	NA
11	0.256	1.8%	No	NA
12	0.230	1.6%	No	NA
13	0.095	0.7%	No	NA
14	0.074	0.5%	No	NA

[a] All PC's with an eigenvalue > 1 were retained

[a] Factors listed are the single factor with the greatest (negative or positive) loading, and the loading value is listed in parentheses

Calculations of Euclidean distance between sample pairs based on PC sample scores did produce somewhat different results between MDE6 watersheds (Table 5.7). While average distance and minimum distance values did not differ substantially between watersheds (Table 5.7), maximum distances were much greater for the Gunpowder and Patapsco than the other 3 watersheds. The range of distance measures indicated that the measure of environmental dissimilarity used in this analysis represented a greater environmental gradient among sample sites within the Gunpowder and Patapsco than the other 3 watersheds.

Table 5.7. Euclidean distance measures between sample site pairs for each MDE6 watershed based on the site scores from the 10 principle components retained from the PCA on habitat and water chemistry variables (Table 5.6).

	Euclidean distance measure		
Watershed	Min	Average	Max
Bush	0.35	4.00	8.89
Gunpowder	0.45	4.02	13.61
Patapsco	0.35	3.95	13.98
Patuxent	0.53	3.87	9.60
Susquehanna	0.55	3.43	9.51

Model selection

The model that incorporated Euclidean geographic distance, the dispersal pathway habitat, and environmental dissimilarity generated the lowest AICc score (Table 5.3). The hypothesis corresponding to this model represents a scenario where local and regional processes both controlled environmental dissimilarity, regional processes related to dispersal were mediated by land use along the dispersal pathway, and regional processes were based on dispersal along the Euclidean pathway. AICc scores ranged from a maximum of -8155.398 (worst model) to a minimum -8713.867 (best model) (Table 5.3). The Δ_i value for the second most supported model (i.e., second lowest AICc score) was 102.045 which provided high support for a single best model (Anderson 2008). The adjusted R^2 values were generally low for all models, with the highest value of 0.1394 occurring for the best model. Providing further support for model selection, the greatest log likelihood value occurred for best model. Variance inflation factors for the 2 models with 3 parameters both indicated that overdispersion was not present in the dataset. The variance inflation factor equals 1 when no multicollinearity is present, and values greater than 10 indicate serious multicollinearity and overdispersion (Kutner et al. 2004). Euclidean geographic distance, Euclidean dispersal pathway habitat, and environmental dissimilarity had variance inflation factors of 1.015, 1.057, and 1.072 respectively for the model that incorporated all three of these variables. Corridor geographic distance, corridor dispersal pathway habitat, and environmental dissimilarity had variance inflation factors of 1.080, 1.072, and 1.011 respectively for the model that incorporated all three of these variables. The Pearson's correlation coefficient calculated for Euclidean distance and environmental dissimilarity was 0.12 and for corridor distance and environmental dissimilarity was 0.10.

Discussion

The importance of regional versus local processes for determining community composition can be tested by examining the relationships of community dissimilarity to geographic distance and environmental dissimilarity (Chase et al. 2005). Community dissimilarity between habitat patches is correlated to geographic distance when regional processes predominate, and community dissimilarity is correlated to environmental dissimilarity when local processes predominate (Nekola and White 1999). Both processes often work simultaneously to determine community composition (Driscoll and Lindenmayer 2009, Cottenie and De Meester 2005, Chase et al. 2005, chapter 3). In addition, the characteristics of an urban landscape may alter dispersal patterns of adult stream insects between streams (chapters 1 and 3, Fahrig 2007). By using multi-model inference testing, I was able to test how well different combinations of variables representing local and regional processes (i.e., geographic distance between sites, dispersal pathway habitat, and environmental dissimilarity) based on different dispersal pathways (Euclidean or corridor distance) explained dissimilarity patterns of stream insect communities between sample site pairs of the MBSS dataset. The multi-model inference testing method could detect if a combination of local and regional factors for different dispersal pathways were important for explaining patterns of community dissimilarity between sample site pairs. The results of the model selection procedure indicated that the best model included Euclidean (i.e., straight line) geographic distance, dispersal pathway habitat, and environmental dissimilarity. This model represented the hypothesis that regional (dispersal) and local (habitat) processes determine stream insect communities, and that land use along dispersal pathways mediated this relationship.

Previous work examining the importance of local and regional processes for determining the composition of stream macroinvertebrate metacommunities found that local factors dominated in headwater reaches (Brown and Swan 2010, Finn and Poff 2011). Thus, limiting the sample site locations to 1st and 2nd order streams should have increased the possibility that local factors were more important for determining community similarity than regional factors. The focus on overland terrestrial dispersal by only including flight capable insect taxa in the analysis likely increased the relevance of regional processes. In addition, sample sites connected longitudinally that could exchange drifting migrants were excluded from the analysis, which increased the focus on overland dispersal.

The shifts in habitat and dispersal ability occurring between developmental stages of stream insects likely make this group susceptible to control by regional and local processes simultaneously in urbanized landscapes. The larval stage of stream insects is long-lived, responsible for the majority of resource acquisition, and closely associated with environmental conditions in the stream. The adult stage is short-lived but responsible for the important life cycle processes of dispersal and reproduction. Bottlenecks to productivity that result in decreased abundance and local extinction can occur through decreased fitness or mortality to either life stage (Huryn and Wallace 2000). Larval fitness is closely tied to the environmental conditions in the stream (basis for environmental dissimilarity), and adult fitness is dependent on the terrestrial landscape, which was represented by geographic distance and the land use along dispersal pathways in the models.

Urban land-use also likely had influences on the strengths of both regional and local processes. Urban land-use can substantially alter the quality of in-stream environmental conditions (Paul and Meyer 2001, Walsh et al. 2005). The sample sites used in this study spanned a gradient of watershed urbanization, and the range of conductivity values indicated that sample sites likely spanned a gradient of stream quality (Roy et al. 2003). The habitat variables included in the assessment of environmental dissimilarity were most likely impacted by watershed urbanization (Paul and Meyer 2001). The differences in these variables across samples is reflected in sample scores of the PC's retained for calculating environmental dissimilarity, and impacts to environmental variables from land use urbanization would be evident in the measures of environmental dissimilarity. Confining the analysis to 1st and 2nd order streams may have limited natural gradients in stream habitat compared to what occurs along a gradient from headwaters to large rivers. The potential for greater impacts to smaller streams (Elmore and Kaushal 2008) from human activities coupled with any environmental similarities across 1st and 2nd order streams may have amplified the differences between streams due to land use urbanization. Thus, alterations to stream habitat and water quality due to human activities in the watershed may have increased the intensity of local processes for structuring stream insect communities, but urban landscapes may have also substantially decreased adult survival and dispersal (chapter 1, chapter 3, Fahrig 2007).

The presence of dispersal pathway habitat in the best model further supported the conclusion that urbanization altered the regional processes structuring communities (Urban et al. 2006). The principle component representing Euclidean dispersal pathway habitat was related to impervious surfaces (represent stream temperature) and percent forested land use. High temperatures and a lack of forested land can have negative impacts on adult insect fitness (Petersen et al. 1999, Collier and Smith 2000, and see chapter 1 for further discussion), and both may have affected the ability of adult stream insects to disperse through terrestrial landscapes (chapter 1). The use of impervious surfaces to represent temperature effects, however, is based on relationships between impervious surfaces and temperature patterns for land and air that are generalized over heterogeneous habitats (Yuan and Bauer 2007, Myint et al. 2010). Air and land temperatures do not describe small spatial scale variations in microclimate temperatures existing in riparian and upland habitat that may affect adult insect survival (Sweeney 1993). In addition, human alterations to the landscape that do not result in impervious surfaces (e.g., golf courses and agriculture) may also make microclimates unsuitable for adult stream insects (Collier and Smith 2000). Impervious surfaces and riparian vegetation were also potentially correlated to small scale landscape characteristics affecting dispersal not considered in this study. Regardless, the inclusion of dispersal pathway habitat in the model with the best fit indicated that urban land use between stream reaches may alter regional processes controlling the structure of stream insect communities.

The importance of environmental dissimilarity in the models further indicated the importance of local in-stream habitat for structuring stream insect communities. The model with environmental dissimilarity alone ranked 5th overall, and it had a lower AICc score (indicating better fit) than the 2 models with a single distance term. In addition, environmental dissimilarity was present in the top 5 models with the best fit. Environmental dissimilarity was not highly correlated to either measure of geographic distance. This indicated that environmental similarity was not redundant with geographic distance and was important for model fit.

The greater fit for the models including Euclidean geographic distance than those including corridor distance suggested that the regional processes controlling community composition are based on dispersal along Euclidean pathways. The highest ranking model including corridor geographic distance (rank = 3) had a Δ_i of 182.931, which indicated a substantially lower amount of support for this model than the best model (Anderson 2008). This model was ranked behind 2 models that included Euclidean geographic distance and environmental dissimilarity. Euclidean and corridor dispersal pathway distances were correlated, and this correlation may have altered the differences in fit between models that incorporated different types of geographic distances. The correlation likely resulted from the exclusion of sample site pairs among different MDE6 watersheds. Examining sample site pairs only from within MDE6 watersheds was done to represent the most plausible condition in which adult insects would disperse between sampling sites. This method excluded sample site pairs on the edges of adjacent MDE6 watersheds that are separated by small Euclidean distances but large corridor distances, but this method also excluded sample site pairs from opposite ends of Maryland's Piedmont that are separated by large Euclidean and corridor distances. The high Δ_i values indicated that fit differed substantially between the top model and the other models, and any decrease in correlation between Euclidean and corridor distances by including sample site pairs among MDE6 watersheds would not have altered the overall results of the model selection procedure.

The belief that adult stream insects disperse through the corridor is based on observational studies of adult abundance along transects perpendicular to the stream channel (Sode and Wideberg-Larsen 1993, Petersen et al. 2004). The results of my study are consistent with the finding by Macneale et al. (2005) that dispersal by flight capable adult stream insects between stream reaches in neighboring watersheds occurs through upland areas. The exclusion of sites occurring up and downstream of each other limits the conclusions of this study to dispersal between watersheds. Dispersal by flight between locations along the same stream may occur along the stream corridor. In addition, spatial autocorrelation based on environmental variables not included in the analysis may have inflated the explanatory power of Euclidean distance.

The analysis used in this study did have drawbacks that may have affected the results. Dissimilarity measures based on taxa presence/absence are less robust than measures that incorporate abundance (Magurran 2004). The data lost by altering the taxonomic resolution and deleting specimens to ensure taxonomic congruence for similarity measures may have affected measures of dissimilarity. In addition, taxonomic composition and dissimilarity patterns indicating local or regional process may have changed during the time period from which the MBSS samples used in this analysis were collected (Finn and Poff 2011, Patrick and Swan 2011). Large scale changes in land use patterns and human impacts to stream systems similar to those reported by Patrick and Swan (2011), however, did not occur during the sampling timeframe analyzed.

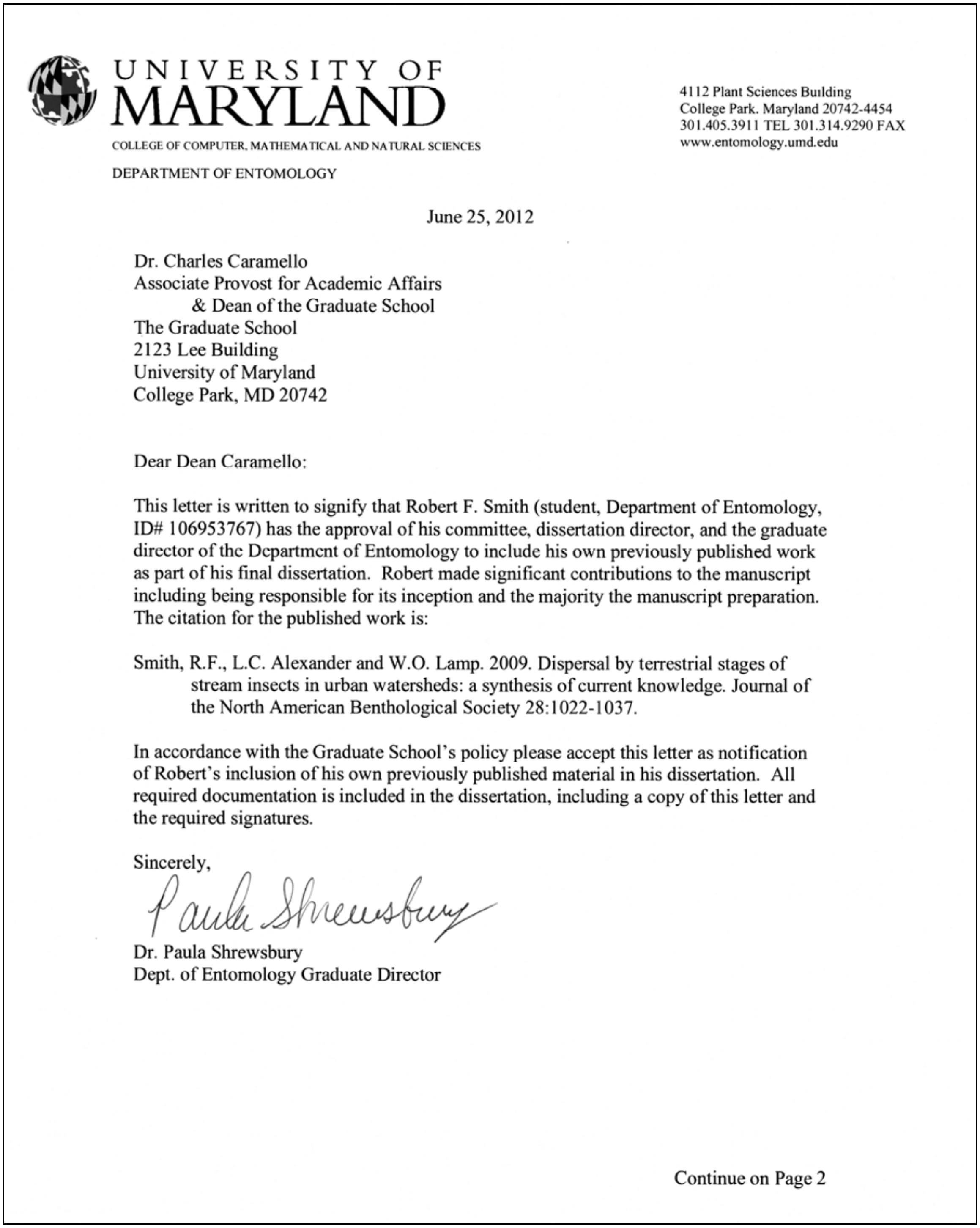
Implications for conservation and restoration

An understanding of the processes structuring communities provides the basis for informed decisions about how best to conserve and restore native biodiversity (Palmer et al. 1997, Young et al. 2005). The results of this study reinforced the conclusion of chapter 3 that restoration and conservation must consider the potential effects urban land use on adult stream insect fitness and dispersal. The potential importance of regional (dispersal mediated) processes for structuring stream insect communities in urbanized landscapes indicates that the decision-making process for prioritizing and assessing stream restoration projects should consider landscape level processes (Palmer et al. 1997, Bond and Lake 2003). The results also suggested that assessments of isolation and colonization potential of stream insect communities should focus on the landscape characteristics along Euclidean dispersal pathways between stream reaches.

Summary

I found that regional and local processes both determined the composition of the stream metacommunity. The models with the greatest support included the Euclidean pathway, which suggested that dispersal along this pathway is more important for structuring communities in neighboring watersheds than dispersal along the corridor. The best model included dispersal pathway habitat, which indicated that land use occurring along the Euclidean dispersal pathway influences regional processes. Urban land use likely intensified the effects of regional and local processes by altering in-stream water and habitat quality, which affects local processes, and by decreasing dispersal and survival of adults, which affects regional processes. Characteristics of urban landscapes likely play a role in structuring stream insect metacommunities in addition to the effects of watershed urbanization on in-stream habitat and water quality. Including the characteristics of the dispersal pathways through urbanized landscapes may be important for determining the importance of local versus regional processes for structuring metacommunities in urbanized landscapes. Regional and local processes should be considered when designing stream restoration and conservation programs.

Appendix A



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June 25, 2012

Dr. Charles Caramello
Associate Provost for Academic Affairs
& Dean of the Graduate School
The Graduate School
2123 Lee Building
University of Maryland
College Park, MD 20742

Dear Dean Caramello:

This letter is written to signify that Robert F. Smith (student, Department of Entomology, ID# 106953767) has the approval of his committee, dissertation director, and the graduate director of the Department of Entomology to include his own previously published work as part of his final dissertation. Robert made significant contributions to the manuscript including being responsible for its inception and the majority the manuscript preparation. The citation for the published work is:

Smith, R.F., L.C. Alexander and W.O. Lamp. 2009. Dispersal by terrestrial stages of stream insects in urban watersheds: a synthesis of current knowledge. Journal of the North American Benthological Society 28:1022-1037.

In accordance with the Graduate School's policy please accept this letter as notification of Robert's inclusion of his own previously published material in his dissertation. All required documentation is included in the dissertation, including a copy of this letter and the required signatures.

Sincerely,

Paula Shrewsbury

Dr. Paula Shrewsbury
Dept. of Entomology Graduate Director

Continue on Page 2

Continued from Page 1

REQUIRED SIGNATURES

Graduate Student

By signing below, the graduate student acknowledge that he/she has satisfied all the requirements of the graduate school for inclusion of their own previously published work in his/her dissertation.

Robert F. Smith Graduate Student, Name	Robert F Smith Signature

Dissertation Committee:

By signing below, the dissertation committee members (including the advisor) acknowledge that the student in question has satisfied all the requirements as described above to include his/her previously published work in his/her dissertation.

William Lamp Dissertation Director (Advisor), Name	Signature
Pedro Barbosa Committee Member 2, Name	P. Barbosa Signature
Daniel Gruner Committee Member 3, Name	Signature
Chris Swan Committee Member 4, Name	Signature
Michael Paul Committee Member 5, Name	Signature
William Higgins Committee Member 6 – Dean's Rep, Name	Signature

Graduate Director

By signing below, the graduate director agrees with the dissertation committee that the student in question has satisfied all the requirements as described above to include his/her previously published work in his/her dissertation.

Paula Shrewsbury Graduate Director (Advisor), Name	Paula Shrewsbury Signature

Appendix B

Malaise trap locations were determined based on a preliminary study examining catch rates for caddisflies at different locations along 1 urban and 1 rural headwater stream (defined as rural and urban based on the same rules described in chapter 2). Malaise traps were placed at an upstream and a downstream location along each stream. At each location, 1 trap was placed across the stream channel perpendicular to flow and suspended above the channel (as described in chapter 2), and 1 trap was placed parallel to the stream channel in the riparian zone directly adjacent to the stream. Traps were left out for 7 to 17 days during a single sampling period for each month between August 2007 and May 2008. Adult caddisflies collected were identified to genus or species.

Traps above the channel collected 100% of the species encountered during the entire preliminary trapping study (Table 6.1). Adult caddisflies were highly abundant in June and July (chapter 2), but preliminary sampling was not done during these months. The extremely low abundances of adult caddisflies caught in the riparian zone at the urban and rural streams during the other months suggested that including samples from June and July would not have altered the conclusions from this preliminary study. As a result of this study, only malaise traps above and perpendicular to the stream channel were used for collecting adult caddisflies for the studies in chapters 2, 3, and 4.

Table 6.1. Taxa richness (genus/species) values for 2007 preliminary survey of adult Trichoptera at 1 rural and 1 urban headwater stream. Data includes 7 to 17 day sampling events per month from August 2007 until May 2008.

Stream type	Total taxa	Trap location	Total taxa	Total abundance	Proportion of total taxa caught
Rural	23	Channel	23	483	100%
		Riparian	7	8	30%
Urban	14	Channel	14	474	100%
		Riparian	4	16	29%

Appendix C

List of taxonomic references used for identifying adult and larval caddisflies for chapters 2, 3, and 4.

Armitage, B. J. 1996. Diagnostic Atlas of the North American Caddisfly Adults I. Philopotamidae. 3rd edition. The Caddis Press, Hilliard, Ohio.

Armitage, B. J. and S. W. Hamilton. 1990. Diagnostic Atlas of the North American Caddisfly Adults II. Ecnomidae, Polycentropodidae, Pyschomyiidae, and Xiphocentronidae. The Caddis Press, Athens, Alabama.

Burington, Z. L. 2011. Larval Taxonomy, Phylogeny and Historical Biogeography of the Genus *Cheumatopsyche* (Trichoptera: Hydropsychidae) in North America. Thesis: Clemson University.

Chapin, J. W. 1978. Systematics of Nearctic *Micrasema* (Trichoptera: Brachycentridae). Dissertation: Clemson University.

Flint, O. S. Jr. 1984. The Genus *Brachycentrus* in North America, with a Proposed Phylogeny of the Genera of Brachycentridae (Trichoptera). Smithsonian Contributions to Zoology, Number 398. Smithsonian Institution Press, Washington, D.C.

Floyd, M. A. 1995. Larvae of the Caddisfly Genus *Oecetis* (Trichoptera: Leptoceridae) in North America. Bulletin of the Ohio Biological Survey, New Series, Vol. 10, No. 3.

Glover, J. B. 1996. Larvae of the Caddisfly Genera *Triaenodes* and *Ylodes* (Trichoptera: Leptoceridae) in North America. Bulletin of the Ohio Biological Survey, New Series, Vol. 11, No. 2.

Keth, A. C. and S. C. Harris. 2008. The North American Genus *Agarodes* Banks (Trichoptera: Sericostomatidae). The Caddis Press, Columbus, Ohio.

Mackay, R. J. 1978. Larval identification and instar association in some species of *Hydropsyche* and *Cheumatopsyche* (Trichoptera: Hydropsychidae). Annals of the Entomological Society of America 71:499-509.

Manuel, K. L. 2010. The Longhorn Caddisfly Genus *Triaenodes* (Trichoptera: Leptoceridae) in North America. The Caddis Press, Columbus, Ohio.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An Introduction to the Aquatic Insects of North America. 4th edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Parker, C. R. and G. B. Wiggins. Revision of the Caddisfly Genus *Psilotreta* (Trichoptera: Odontoceridae). Royal Ontario Museum Life Sciences Contribution 144. Royal Ontario Museum, Toronto, Ontario, Canada.

Prather, A. L. 2001. Eastern Nearctic *Rhyacophila* species, with revision of the *Rhyacophila invaria* group (Trichoptera: Rhyacophilidae). Transactions of the American Entomological Society 127:85-166.

Ross, H. H. 1944. The caddis flies, or Trichoptera, of Illinois. Bulletin of the Illinois Natural History Survey 23:1-326.

Ross, H. H. and D. R. Merkley. 1952. An annotated key to the Nearctic males of *Limnephilus* (Trichoptera: Limnephilidae). The American Midland Naturalist 47:435-455.

Ross, H. H. and D. C. Scott. 1974. A review of the caddisfly genus *Agarodes*, with descriptions of new species (Trichoptera: Sericostomatidae). Journal of the Georgia Entomological Society 9:147-155.

Ross, H. H. and J. B. Wallace. 1974. The North American genera of the family Sericostomatidae (Trichoptera). Journal of the Georgia Entomological Society 9:42-48.

Ruiter, D. E. 1995. The Genus *Limnephilus* Leach (Trichoptera: Limnephilidae) of the New World. Vol. 11. Ohio Biological Survey, College or Biological Sciences, Ohio State University, Columbus, Ohio.

Ruiter, D. E. 2000. Generic Key to the Adult Ocellate Limnephiloidea of the Western Hemisphere (Insecta: Trichoptera). Miscellaneous Contributions Number 5. Ohio Biological Survey, College or Biological Sciences, Ohio State University, Columbus, Ohio.

Schefter, P. W. and G. B. Wiggins. 1986. A Systematic Study of the Nearctic Larvae of the *Hydropsyche morosa* Group (Trichoptera: Hydropsychidae). Royal Ontario Museum Life Sciences Miscellaneous Publications. Royal Ontario Museum, Toronto, Ontario, Canada.

Schmid, F. 1998. The Insects and Arachnids of Canada. Part 7. Genera of the Trichoptera of Canada and Adjoining or Adjacent United States. NRC Research Press, Ottawa, Ontario, Canada.

Schuster, G. A. and D. A. Etnier. 1978. A Manual for the Identification of the Larvae of the Caddisfly Genera *Hydropsyche* Pictet and *Symphitopsyche* Ulmer in Eastern and Central North America (Trichoptera: Hydropsychidae). Environmental Monitoring and Support Laboratory, US EPA, Cincinnati Ohio. EPA-600/4-78-060

Sherberger, F. F. and J. B. Wallace. 1971. Larvae of the southeastern species of *Molanna*. Journal of the Kansas Entomological Society 44:217-224.

Vineyard, R. N., G. B. Wiggins, H. E. Frania, and P. W. Schefter. 2005. The Caddisfly Genus *Neophylax* (Trichoptera: Uenoidae). Royal Ontario Museum Contributions in Science, 2. Royal Ontario Museum, Toronto, Ontario, Canada.

Weaver, J. S. III. 1988. A synopsis of the North American Lepidostomatidae (Trichoptera). Contributions of the American Entomological Institute 24:1–141.

Wiggins, G. B. 1997. The Caddisfly Family Phryganeidae (Trichoptera). University of Toronto Press, Toronto, Ontario, Canada.

Wiggins, G. B. 1998. Larvae of the North American Caddisfly Genera (Trichoptera). 2nd edition. University of Toronto Press, Toronto, Ontario, Canada.

Appendix D

Three male specimens of each species collected, or however many male specimens were collected if less than 3, had their DNA barcoded and cross referenced against the BOLD system database. Exact methods are identical to those reported in Pilgrim et al. (2011). In summary, tissue from 1 or 2 legs (usually the hind leg) was removed, placed in BIO-RAD 96-well plates (Bio-Rad Laboratories, Hercules, California), and sent overnight to the US Environmental Protection Agency (EPA) lab in Cincinnati, Ohio for analysis. The Folmer region of cytochrome c oxidase subunit I (COI) deoxyribonucleic acid (DNA) was amplified by polymerase chain reaction (PCR), and the product was sequenced in both directions using a capillary sequencer (3730xl DNA Analyzer; Applied Biosystems). Raw sequences were analyzed with Sequencher (v 4/7; Gene Codes Corp, Ann Arbor, Michigan) to create a contig that was submitted to the BOLD system database. The database returned a percent match to previously submitted DNA barcodes for identified taxa. A 97% match was considered a conclusive match of the submitted specimen to the species in the BOLD database. Taxa without a conclusive match to specimens in the BOLD database and could not be identified with taxonomic keys were assigned a morphospecies designation. Specimens were assigned to a multispecies complex (i.e., spp.) when more than one taxa was conclusively linked to a group of specimens that could not be reliably separated using morphological characters.

DNA barcoding aided the identifications needed for assessing differences in communities and populations of adult caddisflies at urban and rural headwater streams. Increased confidence in species level identifications from DNA barcoding allowed for increased precision of taxonomic data. DNA barcoding and traditional morphological based taxonomic methods complemented each other to increase the information gained from surveys of adult caddisflies. The success and efficiency of this method showed that combining barcoding and traditional taxonomy can improve studies of basic ecology and is not just suited for applied work (Pilgrim et al. 2011).

References Cited

Ahlroth, P., R. V. Alatalo, A. Holopainen, T. Kumpulainen, and J. Suhonen. 2003. Founder population size and number of source populations enhance colonization success in waterstriders. Oecologia (Berlin) 442:617-620.

Alexander, L. C., D. J. Hawthorne, M. A. Palmer, and W. O. Lamp. 2011. Loss of genetic diversity in the North American mayfly *Ephemerella invaria* associated with deforestation of headwater streams. Freshwater Biology 56:1456-1467.

Alexander, S., and L. A. Smock. 2005. Life histories and production of *Cheumatopsyche analis* and *Hydropsyche betteni* (Trichoptera: Hydropsychidae) in an urban Virginia stream. Northeastern Naturalist 12:433-446.

Allan, J. D. 1995. Stream ecology. Kluwer Academic Publishers, Boston, Massachusetts.

Allan, J. D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology, Evolution, and Systematics 35:257-284.

Allan, J. D., and A. S. Flecker. 1993. Biodiversity conservation in running waters. BioScience 43:32-43.

Almbro, M. and C. Kullberg. 2008. Impaired escape flight ability in butterflies due to low flight muscle ratio prior to hibernation. The Journal of Experimental Biology 211:24-28.

Altizer, W. and A. K. Davis. 2010. Populations of Monarch butterflies with different migratory behaviors show divergence in wing morphology. Evolution (online first article):1-11.

Anderson, D. R. 2008. Model based inference in the life sciences: A primer on evidence. Spring Science + Business Media, LLC, New York, NY.

Anholt, B. R. 1995. Density dependence resolves the stream drift paradox. Ecology 76:2235-2239.

Banks, J. L., J. Li, and A. T. Herlihy. 2007. Influence of clearcut logging, flow duration, and season on emergent aquatic insects in headwater streams of the Central Oregon Coast Range. Journal of the North American Benthological Society 26:620-632.

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish. 2nd edition. EPA 841-B-99-002. Office of Water, US Environmental Protection Agency, Washington, DC.

Beck, M. W. 1995. Size-specific shelter limitation in stone crabs: A test of the demographic bottleneck hypothesis. Ecology 76:968-980.

Benke, A. C. 1996. Secondary production of macroinvertebrates. Pp 557-578. In F. R. Hauer and G. A. Lamberti (editors), Methods In Stream Ecology. Academic Press, New York.

Bernáth, B., G. Szedenics, H. Wildermuth, and G. Horváth. 2002. How can dragonflies discern bright and dark waters from a distance? The degree of polarisation of reflected light as a possible clue for dragonfly habitat selection. Freshwater Biology 47:1707-1719.

Berwaerts, K., H. Van Dyck, and P. Aerts. 2002. Does flight morphology relate to flight performance? An experimental test with the butterfly *Pararge aegeria*. Functional Ecology 16:484-491.

Bilton, D. T., J. R. Freeland, and B. Okamura. 2001. Dispersal in freshwater invertebrates. Annual Review of Ecology and Systematics 32:159–181.

Blakely, T. J., J. S. Harding, A. R. McIntosh, and M. J. Winterbourn. 2006. Barriers to the recovery of aquatic insect communities in urban streams. Freshwater Biology 51:1634-1645.

Bonada, N., N. Prat, V. H. Resh, and B. Statzner. 2006. Developments in aquatic insect biomonitoring: A comparative analysis of recent approaches. Annual Review of Entomology 51:495-523.

Bond, N. R., and P. S. Lake. 2003. Local habitat restoration in streams: Constraints on the effectiveness of restoration for stream biota. Ecological Management and Restoration 4:193-198.

Boward, D. and E. Friedman. 2011. Maryland Biological Stream Survey Laboratory Methods for Benthic Macroinvertebrate Processing and Taxonomy. Maryland Department of Natural Resources report# CBWP-MANTA-EA-00-6 (revised 2011). Annapolis, MD.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. Biological Reviews 80:205-225.

Brady, V. J., B. J. Cardinale, J. P.Gathman, and T. M. Burton. 2002. Does facilitation of faunal recruitment benefit ecosystem restoration? An experimental study of invertebrate assemblages in wetland mesocosms. Restoration Ecology 10:617-626.

Briers, R. A., H. M. Cariss, and J. H. R. Gee. 2002. Dispersal of adult stoneflies (Plecoptera) from upland streams draining catchments with contrasting land-use. Archiv für Hydrobiologie 155:627-644.

Briers, R. A., H. M. Cariss, and J. H. R. Gee. 2003. Flight activity of adult stoneflies in relation to weather. Ecological Entomology 28:31-40.

Briers, R. A., H. M. Cariss, R. Geoghegan, and J. H. R. Gee. 2005. The lateral extent of the subsidy from an upland stream to riparian lycosid spiders. Ecography 28: 165-170.

Briers, R. A., and J. H. R. Gee. 2004. Riparian forestry management and adult stream insects. Hydrology and Earth System Sciences 8:545-549.

Briers, R. A., J. H. R. Gee, H. M. Cariss, and R. Geoghegan. 2004. Inter-population dispersal by adult stoneflies detected by stable isotope enrichment. Freshwater Biology 49:425-431.

Brittain, J. E. 1982. Biology of mayflies. Annual Review of Entomology 27:119-147.

Brown, B. L. and C. M. Swan. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. Journal of Animal Ecology. 79:517-580.

Brown, B. L., C. M. Swan, D. A. Auerbach, E. H. Campbell Grant, N. P. Hitt, K. O. Maloney, and C. Patrick. 2011. Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. Journal of the North American Benthological Society 30:310-327.

Bunn, S. E., and J. M. Hughes. 1997. Dispersal and recruitment in streams: Evidence from genetic studies. Journal of the North American Benthological Society 16: 338-346.

Byrne, D.N., S.L. Buchmann, and H.G. Spangler. 1988. Relationship between wing loading, wingbeat frequency and body mass in homopterous insects. Journal of Experimental Biology 135:9-23.

Cadotte, M. W. 2006. Dispersal and species diversity: A meta-analysis. The American Naturalist 167:913-924.

Calabrese, J. M. and W. F. Fagan. 2004. Lost in time, lonely, and single: Reproductive asynchrony and the Allee Effect. The American Naturalist 164:25-37.

Caudill, C. C. 2003. Empirical evidence for nonselective recruitment and a source-sink dynamic in a mayfly metapopulation. Ecology 84:2119-2132.

Chan, E. K. W., Y. Zhang, and D. Dudgeon. 2007. Contribution of adult aquatic insects to riparian prey availability along tropical forest streams. Marine and Freshwater Research 58:725-732.

Chapman, R. F. 1998. The insects: Structure and function. 4th edition. Cambridge University Press, New York.

Chaput-Bardy, A., C. Lemaire, D. Picard, and J. Secondi. 2008. In-stream and overland dispersal across a river network influences gene flow in a freshwater insect, *Calopteryx splendens*. Molecular Ecology 17:3496-3505.

Chase, J. M., P. Amarasekare, K. Cottenie, A. Gonzalez, R. D. Holt, M. Holyoak, M. F. Hoopes, M. A. Leibold, M. Loreau, N. Mouquet, J. B. Shurin, and D. Tilman. 2005. Competing theories for competitive metacommunities. Pages 335-354 in M.

Holyoak, M. A. Leibold, and R. D. Holt (editors). Metacommunities: Spatial Dynamics and Ecological Communities. The University of Chicago Press, Chicago, IL.

Cain, S. A. 1938. The species-area curve. American Midland Naturalist. 19:573-581.

Clarke, A., R. Mac Nally, N. Bond, and P. S. Lake. 2008. Macroinvertebrate diversity in headwater streams: A review. Freshwater Biology 53:1707-1721.

Cao, Y. and C. P. Hawkins. 2011. The comparability of bioassessments: A review of conceptual and methodological issues. Journal of the North American Benthological Society 30:680-701.

Collier, K. J., and B. J. Smith. 1998. Dispersal of adult caddisflies (Trichoptera) into forests alongside three New Zealand streams. Hydrobiologia 361:53-65.

Collier, K. J., and B. J. Smith. 2000. Interactions of adult stoneflies (Plecoptera) with riparian zones I. Effects of air temperature and humidity on longevity. Aquatic Insects 22:275-284.

Collier, K. J., B. J. Smith, and B. R. Baillie. 1997. Summer light-trap catches of adult Trichoptera in hill-country catchments of contrasting land use, Waikato, New Zealand. New Zealand Journal of Marine and Freshwater Research 31:623-634.

Corbet, P. S. 1999. Dragonflies: Behavior and ecology of Odonata. Harley Books, Colchester, UK.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175-1182.

Cottenie, K., and L. De Meester. 2005. Local interactions and local dispersal in a zooplankton metacommunity. Pages 189-211 in M. Holyoak, M. A. Leibold, and

R. D. Holt (editors). Metacommunities: Spatial Dynamics and Ecological Communities. The University of Chicago Press, Chicago, IL.

Coutant, C. C. 1982. Evidence for upstream dispersion of adult caddisflies (Trichoptera: Hydropsychidae) in the Columbia River. Aquatic Insects 4:61-66.

Covich, A. P., M. A. Palmer, and T. A. Crowl. 1999. The role of benthic invertebrate species in freshwater ecosystems: Zoobenthic species influence energy flows and nutrient cycling. BioScience 49:119-127.

Davies, K. F., C. Gascon, and C. R. Margules. 2001. Habitat fragmentation: consequences, management, and future research priorities. Pages 81-97 in M. E. Soule´ and G. H. Orians (editors). Conservation biology: research priorities for the next decade. Island Press, Washington, DC.

De Block, M. and R. Stoks. 2008. Compensatory growth and oxidative stress in a damselfly. Proceedings of The Royal Society B - Biological Sciences 275:781-785.

Delettre, Y. R., and N. Morvan. 2000. Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. Freshwater Biology 44:399-411.

Dias, P. C. 1996. Sources and sinks in population biology. Trends in Ecology and Evolution 11:326-330.

Driscoll, D. A., and D. B. Lindenmayer. 2009. Empirical tests of metacommunity theory using an isolation gradient. Ecological Applications 79:485-501.

Dunnett, C. W. 1980. Pairwise multiple comparisons in the unequal variance case. Journal of the American Statistical Association 75:796-800.

Eisenbeis, G. 2006. Artificial night lighting and insects: Attraction of insects to streetlamps in a rural setting in Germany. Pages 281-304 in C. Rich and T. Longcore (editors). Ecological consequences of artificial night lighting. Island Press, Washington, DC.

Elliot, J. M. 2003. A comparative study of the dispersal of 10 species of stream invertebrates. Freshwater Biology 48:1652-1668.

Elliott, G. G. and M. L. Evenden. 2009. Factors influencing flight potential of *Choristoneura conflictana*. Physiological Entomology 34:71-78.

Elmore, A. J., and S. S. Kaushal. 2008. Disappearing headwaters: Patterns of stream burial due to urbanization. Frontiers in Ecology and the Environment 6:308-312.

Encalada, A. C., and B. L. Peckarsky. 2006. Selective oviposition of the mayfly *Baetis bicaudatus*. Oecologia (Berlin) 148:526-537.

Enders, G., and R. Wagner. 1996. Mortality of *Apatania fimbriata* (Insecta: Trichoptera) during embryonic, larval and adult life stages. Freshwater Biology 36:93-104.

Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81:117-142.

Faeth, S. H., P. S. Warren, E. Shochat, and W. A. Marussich. 2005. Trophic dynamics in urban communities. BioScience 55:399-407.

Fagan, W. F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83:3243-3249.

Fagan, W. F., C. Aumann, C. M. Kennedy, and P. J. Unmack. 2005. Rarity, fragmentation, and the scale dependence of extinction risk in desert fishes. Ecology 86:34-41.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics 34:487-515.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21:1003-1015.

Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival. Ecology 66:1762-1768.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8:50-59.

Finn, D. S. and N. L. Poff. 2008. Emergence and flight activity of alpine stream insects in two years with contrasting winter snowpack. Arctic, Antarctic, and Alpine Research 40:638-646.

Finn, D. S., D. M. Theobald, I. Black, W.C., and N. L. Poff. 2006. Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. Molecular Ecology 15:3553-3566.

Finn, D. S., M. S. Blouin, and D. A. Lytle. 2007. Population genetic structure reveals terrestrial affinities for a headwater stream insect. Freshwater Biology 52:1881-1897.

Finn, D. S. and N. L. Poff. 2011. Examining spatial concordance of genetic and species diversity patterns to evaluate the role of dispersal limitation in structuring headwater metacommunities. Journal of the North American Benthological Society 30:273-283.

Frankel, O. H., and M. E. Soulé. 1981. Conservation and evolution. Cambridge University Press, Cambridge, UK.

Fuchs, U., and B. Statzner. 1990. Time scales for the recovery potential of river communities after restoration: Lessons to be learned from smaller streams. Regulated Rivers: Research and Management 5:77-87.

Fukui, D., M. Murakami, S. Nakano, and T. Aoi. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. Journal of Animal Ecology 75:1252-1258.

Funk, D. H., J. K. Jackson, and B. W. Sweeney. 2006. Taxonomy and genetics of the parthenogenetic mayfly *Centroptilum triangulifer* and its sexual sister *Centroptilum alamance* (Ephemeroptera:Baetidae). Journal of the North American Benthological Society 25:417-429.

Gandon, S., and Y. Michalakis. 2001. Multiple causes of the evolution of dispersal. Pages 155-167 in J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols (editors). Dispersal. Oxford University Press, Oxford, UK.

Gomi, T., R. C. Sidle, and J. S. Richardson. 2002. Understanding processes and downstream linkages of headwater systems. BioScience 52:905-916.

Gooderham, J. P. R., L. A. Barmuta, and P. E. Davies. 2007. Upstream heterogeneous zones: Small stream systems structured by a lack of competence? Journal of the North American Benthological Society 26:365-374.

Goretti, E., D. Ceccagnoli, M.V. Di Giovanni. 2005. Morphometric pattern and biometry of adult Trichoptera (Italian species). Italian Journal of Zoology 72:15-19.

Grant, E. H. C., W. H. Lowe, and W. F. Fagan. 2007. Living in the branches: Population and ecological processes in dendritic networks. Ecology Letters 10:165-175.

Gray, L. J. 1989. Emergence production and export of aquatic insects from a tallgrass prairie stream. Southwestern Naturalist 34:313-318.

Gray, L. J. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. American Midland Naturalist 129:288-300.

Grenouillet, G., S. Brosse, L. Tudesque, S. Lek, Y. Baraillé, and G. Loot. 2008. Concordance among stream assemblages and spatial autocorrelation along a fragmented gradient. Diversity and Distributions 14:592-603.

Griffith, M. B., E. M. Barrows, and S. A. Perry. 1998. Lateral dispersal of adult aquatic insects (Plecoptera, Trichoptera) following emergence from headwater streams in forested Appalachian catchments. Annals of the Entomological Society of America 91:195-201.

Hanski, I. 1998. Metapopulation dynamics. Nature 396:41-49.

Harrison, S. S. C., and I. T. Harris. 2002. The effects of bankside management on chalk stream invertebrate communities. Freshwater Biology 47:2233-2245.

Heino, J., T. Muotka, H.Mykrä, R. Paavola, H. Hämäläinen, and E. Koskenniemi. 2003a. Defining macroinvertebrate assemblage types of headwater streams: Implications for bioassessment and conservation. Ecological Applications 13:842-852.

Heino, J., T. Muotka, and R. Paavola. 2003b. Determinants of macroinvertebrate diversity in headwater streams: Regional and local influences. Journal of Animal Ecology 72:425-434.

Heino, J., J. Parviainen, R. Paavola, M. Jehle, P. Louhi, and T. Muotka. 2005. Characterizing macroinvertebrate assemblage structure in relation to stream size and tributary position. Hydrobiologia 539:121-130.

Hershey, A. E., J. Pastor, B. J. Peterson, and G. W. Kling. 1993. Stable isotopes resolve the drift paradox for *Baetis* mayflies in an Arctic river. Ecology 74:2315-2325.

Hoffman, R. S., P. D. Capel, and S. J. Larson. 2000. Comparison of pesticides in eight U.S. urban streams. Environmental Toxicology and Chemistry 19:2249-2258.

Hoffmann, A. 2000. The association of the stream caddisfly *Lasiocephala basalis* (Kol.) (Trichoptera: Lepidostomatidae) with wood. International Review of Hydrobiology 85:79-93.

Hoffmann, A., and V. H. Resh. 2003. Oviposition in three species of limnephiloid caddisflies (Trichoptera): Hierarchical influences on site selection. Freshwater Biology 48:1064-1077.

Hoffsten, P. 2004. Site-occupancy in relation to flight morphology in caddisflies. Freshwater Biology 49:810-817.

Horrigan, N., and D. J. Baird. 2008. Trait patterns of aquatic insects across gradients of flow-related factors: A multivariate analysis of Canadian national data. Canadian Journal of Fisheries and Aquatic Sciences 65:670-680.

Horváth, G., and D. Varjú. 1997. Polarization pattern of freshwater habitats recorded by video polarimetry in red, green, and blue spectral ranges and its relevance for water detection by aquatic insects. Journal of Experimental Biology 200:1155-1163.

Horváth, G., P. Malik, G. Kriska, and H. Wildermuth. 2007. Ecological traps for dragonflies in a cemetery: The attraction of *Sympetrum* species (Odonata: Libellulidae) by horizontally polarizing black gravestones. Freshwater Biology 52:1700-1709.

Hughes, J. M. 2007. Constraints on recovery: Using molecular methods to study connectivity of aquatic biota in rivers and streams. Freshwater Biology 52:616-631.

Hughes, J. M., S. E. Bunn, C. Cleary, and D. A. Hurwood. 2000a. A hierarchical analysis of the genetic structure of an aquatic insect *Bungona* (Baetidae: Ephemeroptera). Heredity 85:561-570.

Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Moltchaniwsky, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 2000b. Supply-side ecology works both ways: The link between benthic adults, fecundity, and larval recruits. Ecology 81:2241-2249.

Huryn, A. D., and J. B. Wallace. 2000. Life history and production of stream insects. Annual Review of Entomology 45:83-110.

Huryn, A. D., J. B. Wallace, and N. H. Anderson. 2008. Habitat, life history, secondary production, and behavioral adaptations of aquatic insects. Pages 55–103 in R. W. Merritt, K. W. Cummins, and M. B. Berg (editors). An introduction to the aquatic insects of North America. 4th edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Huxel, G. R., and A. Hastings. 1999. Habitat loss, fragmentation, and restoration. Restoration Ecology 7:309-315.

Hynes, H. B. N. 1976. Biology of Plecoptera. Annual Review of Entomology 21:135-153.

Ims, R. A. and D. Ø. Hjermann. 2001. Condition dependent dispersal. Pages 203-216 in J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols (editors). Dispersal. Oxford University Press, Oxford, UK.

Ims, R. A. and N. G. Yoccoz. 1997. Studying transfer processes in metapopulations. In: Hanski, I. and Gilpin, M. E. (eds.), Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, pp. 247-265.

Jackson, J. K. 1988. Diel emergence, swarming and longevity of selected adult aquatic insects from a Sonoran desert stream. American Midland Naturalist 119:344-352.

Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. Ecology 67:629-638.

Jackson, J. K., E. P. McElravy, and V. H. Resh. 1999. Longterm movements of self-marked caddisfly larvae (Trichoptera: Sericostomatidae) in a California coastal mountain stream. Freshwater Biology 42:525-536.

Jackson, J. K., and V. H. Resh. 1989. Distribution and abundance of adult aquatic insects in the forest adjacent to a northern California stream. Environmental Entomology 18:278–283.

Jacobson, B., and P. R. Peres-Neto. 2010. Quantifying and disentangling dispersal in metacommunities: How close have we come? How far is there to go? Landscape Ecology 25:495-507.

Jáimez-Cuéllar, P., and J. M. Tierno de Figueroa. 2005. Local emergence distribution patterns of *Dinocras cephalotes* (Plecoptera, Perlidae). Biologia 60:539-543.

Jannot, J. E., E. Bruneau, and S. A. Wissinger. 2007. Effects of larval energetic resources on life history and adult allocation patterns in a caddisfly (Trichoptera: Phryganeidae). Ecological Entomology 32:376-383.

Jansson, R., C. Nilsson, and B. Malmqvist. 2007. Restoring freshwater ecosystems in riverine landscapes: The roles of connectivity and recovery processes. Freshwater Biology 52:589-596.

Kaitala, A., and L. Huldén. 1990. Significance of spring migration and flexibility in flight-muscle histolysis in waterstriders (Heteroptera, Gerridae). Ecological Entomology 15:409-418.

Karr, J. R. 1999. Defining and measuring river health. Freshwater Biology 41:221-234.

Kato, C., T. Iwata, S. Nakano, and D. Kishi. 2003. Dynamics of aquatic insect flux affects distribution of riparian web-building spiders. Oikos 103:113-120.

Kelly, L. C., D. T. Bilton, and S. D. Rundle. 2001. Population structure and dispersal in the Canary Island caddisfly *Mesophylax aspersus* (Trichoptera, Limnephilidae). Heredity 86:370–377.

Klauda, R., P. Kazyak, S. Stranko, M. Southerland, N. Roth, and J. Chaillou. 1998. Maryland biological stream survey: A state agency program to assess the impact of anthropogenic stresses on stream habitat quality and biota. Environmental Monitoring and Assessment 51:299-316.

Kominoski, J. S., S. Larrañaga, and J. S. Richardson. 2012. Invertebrate feeding and emergence timing vary among streams along a gradient of riparian forest composition. Freshwater Biology 57:759-772.

Kovats, Z. E., J. J. H. Ciborowski, and L. D. Corkum. 1996. Inland dispersal of adult aquatic insects. Freshwater Biology 36:265-276.

Kriska, G., G. Horváth, and S. Andrikovics. 1998. Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts Ephemeroptera. Journal of Experimental Biology 201:2273-2286.

Kriska, G., Z. Csabai, P. Boda, P. Malik, and G. Horváth. 2006. Why do red and dark-coloured cars lure aquatic insects? The attraction of water insects to car paintwork explained by reflection-polarization signals. Proceedings of the Royal Society of London Series B: Biological Sciences 273:1667-1671.

Kriska, G., P. Malik, I. Szivák, and G. Horváth. 2008. Glass buildings on river banks as ‘‘polarized light traps’’ for mass-swarming polarotactic caddis flies. Naturwissenschaften 95:461-467.

Kristan, W. B. 2003. The role of habitat selection behavior in population dynamics: Source-sink systems and ecological traps. Oikos 103:457-468.

Kutner, M. H., Nachtsheim, C. J., and J. Neter. 2004. Applied Linear Regression Models. Fourth edition. McGraw-Hill/Irwin, New York, NY.

Lake, P. S., N. Bond, and P. Reich. 2007. Linking ecological theory with stream restoration. Freshwater Biology 52: 597-615.

Lancaster, J., B. J. Downes, and P. Reich. 2003. Linking landscape patterns of resource distribution with models of aggregation in ovipositing stream insects. Journal of Animal Ecology 72:969-978.

Legendre, P. and L. Legendre. 1998. Numerical Ecology. 2nd edition. Elsevier Science, Amsterdam, The Netherlands.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004.

The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7:601-613.

Lepš, J., and P. Šmilauer. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, New York.

Li, J. L., S. L. Johnson, and J. B. Sobota. 2011. Three responses to small changes in stream temperature by autumn-emerging aquatic insects. Journal of the North American Benthological Society 30:474-484.

Lindhe Norberg, U.M. 2002. Structure, form, and function of flight in engineering and the living world. Journal of Morphology 252:52-81.

Loreau, M. 2000. Are communities saturated? On the relationship between α, β, and γ diversity. Ecology Letters 3:73-76.

Lövei, G. L., A. Macleod, and J. M. Hickman. 1998. Dispersal and effects of barriers on the movement of the New Zealand hover fly *Melanostoma fasciatum* (Dipt., Syrphidae) on cultivated land. Journal of Applied Entomology 122:115-120.

Lowe, W. H. 2002. Landscape-scale spatial population dynamics in human-impacted stream systems. Environmental Management 30:225-233.

Lowe, W. H. 2009. What drives long-distance dispersal? A test of theoretical predictions. Ecology 90:1456-1462.

Lowe, W. H., K. H. Nislow, and D. T. Bolger. 2004. Stage-specific and interactive effects of sedimentation and trout on a headwater stream salamander. Ecological Applications 14:164-172.

Lowe, W. H., G. E. Likens, and M. E. Power. 2006. Linking scales in stream ecology. BioScience 56:591-597.

Lynch, R. J., S. E. Bunn, and C. P. Catterall. 2002. Adult aquatic insects: Potential contributions to riparian food webs in Australia's wet-dry tropics. Austral Ecology 27: 515-526.

Mackay, R. J. 1992. Colonization by lotic macroinvertebrates: A review of processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences 49:617-628.

Macneale, K. H., B. L. Peckarsky, and G. E. Likens. 2004. Contradictory results from different methods for measuring direction of insect flight. Freshwater Biology 49: 1260-1268.

Macneale, K. H., B. L. Peckarsky, and G. E. Likens. 2005. Stable isotopes identify dispersal patterns of stonefly populations living along stream corridors. Freshwater Biology 50:1117-1130.

Mader, H. J., C. Schell, and S. P. Kornacker. 1990. Linear barriers to arthropod movements in the landscape. Biological Conservation 54:209-222.

Magurran, A. E. 2004. Measuring Biological Diversity. Blackwell Publishing Ltd, Malden, MA.

Malmqvist, B. 2000. How does wing length relate to distribution patterns of stoneflies (Plecoptera) and mayflies (Ephemeroptera)? Biological Conservation 93:271-276.

Marden, J. H. 2000. Variability in the size, composition, and function of insect flight muscles. Annual Review of Physiology 62:157-178.

Masters, Z., I. Peteresen, A. G. Hildrew, and S. J. Ormerod. 2007. Insect dispersal does not limit the biological recovery of streams from acidification. Aquatic Conservation: Marine and Freshwater Ecosystems 17:375-383.

McIntyre, N. E. 2000. Ecology of urban arthropods: A review and a call to action. Annals of the Entomological Society of America 93:825-835.

McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. BioScience 52:883-890.

Menge, B. A. 2000. Recruitment vs. postrecruitment processes as determinants of barnacle population abundance. Ecological Monographs 70:265-288.

Meyer, J. L., R. Beilfuss, Q. Carpenter, L. A. Kaplan, D. Newbold, R. Semlitsch, D. L. Strayer, M. C. Watzin, C. J. Woltemade, J. B. Zedler, and P. H. Zedler. 2003. Where rivers are born: The scientific imperative for defending small streams and wetlands. Washington D.C.

Meyer, J. L., D. L. Strayer, J. B. Wallace, S. L. Eggert, G. S. Helfman, and N. E. Leonard. 2007. The contribution of headwater streams to biodiversity in river networks. Journal of the American Water Resources Association 43:86-103.

Moglen, G. E. 2005. GISHydro2000: a tool for automated hydrologic analysis in Maryland. Page 51 in G. E. Moglen (editor). Managing watersheds for human and natural impacts: engineering, ecological, and economic challenges 2005. American Society of Civil Engineers, Reston, Virginia.

Moore, A. A., and M. A. Palmer. 2005. Invertebrate biodiversity in agricultural and urban headwater streams: Implications for conservation and management. Ecological Applications 15:1169-1177.

Morgan, R. P. and S. F. Cushman. 2005. Urbanization effects on stream fish assemblages in Maryland, USA. Journal of the North American Benthological Society 24:643-655.

Morin, P. J. 1999. Community Ecology. Blackwell Science, Malden, MA.

Morse, J.C. and R.W. Holzenthal. 2008. Trichoptera Genera. Pages 481-552 in R.W. Merritt, K.W. Cummins, and M.B. Berg (editors). An Introduction to the Aquatic Insects of North America. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Müller, K. 1982. The colonization cycle of freshwater insects. Oecologia (Berlin) 52:202-207.

Myint, S. W., A. Brazel, G. Okin, and A. Buyantuyev. 2010. Combined effects of impervious surface and vegetation cover on air temperature variations in a rapidly expanding desert city. GIScience and Remote Sensing 47:301-320.

Neves, R. J. 1979. Movements of larval and adult *Pycnopsyche guttifer* (Walker) (Trichoptera: Limnephilidae) along Factory Brook, Massachusetts. American Midland Naturalist 102:51-58.

Ocampo, C. B., and D. M. Wesson. 2004. Population dynamics of *Aedes aegypti* from a Dengue hyperendemic urban setting in Colombia. American Journal of Tropical Medicine and Hygiene 71:506-513.

Oke, T. R. 1989. The micrometeorology of the urban forest. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 324:335-349.

Paetzold, A., and K. Tockner. 2005. Effects of riparian arthropod predation on the biomass and abundance of aquatic insect emergence. Journal of the North American Benthological Society 24:395-402.

Palmer, M. A., J. D. Allan, and C. A. Butman. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. Trends in Ecology and Evolution 11:322-326.

Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological theory and community restoration ecology. Restoration Ecology 5:291-300.

Patrick, C. J. and C. M. Swan. 2011. Reconstructing the assembly of a stream-insect metacommunity. Journal of the North American Benthological Society 30:259-272.

Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32:333-365.

Payne, J. C., and J. E. Dunley. 2002. Use of an elemental marker, rubidium, to study dispersal of aquatic insects. Journal of the North American Benthological Society 21:715-727.

Pearson, W. D., and R. H. Kramer. 1972. Drift and production of two aquatic insects in a mountain stream. Ecological Monographs 42:365-385.

Peckarsky, B. L., B. W. Taylor, and C. C. Caudill. 2000. Hydrologic and behavioral constraints on oviposition of stream insects: Implications for adult dispersal. Oecologia (Berlin) 125:186-200.

Perkin, E. K., F. Hölker, J. S. Richardson, J. P. Sadler, C. Wolter, and K. Tockner. 2011. The influence of artificial light onstream and riparian ecosystems: Questions, challenges, and perspectives. Ecosphere 2:122.

Petersen, I., and A. G. Hildrew. 2003. Emergence of *Leuctra nigra* (Plecoptera) from a southern English stream. Archiv für Hydrobiologie 158:185-195.

Petersen, I., J. H. Winterbottom, S. Orton, N. Friberg, A. G. Hildrew, D. C. Spiers, and W. S. C. Gurney. 1999. Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, U.K. Freshwater Biology 42:401-416.

Petersen, I., Z. Masters, A. G. Hildrew, and S. J. Ormerod. 2004. Dispersal of adult aquatic insects in catchments of differing land use. Journal of Applied Ecology 41:934-950.

Petersson, E. 1989. Swarming activity patterns and seasonal decline in adult size in some caddis flies (Trichoptera: Leptoceridae). Aquatic Insects 11:17-28.

Petersson, E., and A. T. Hasselrot. 1994. Mating and nectar feeding in the psychomyiid caddis fly *Tinodes waeneri*. Aquatic Insects 16:177-187.

Pickett, S. T. A., M. L. Cadenasso, J. M. Grove, C. H. Nilon, R. V. Pouyat, W. C. Zipperer, and R. Costanza. 2001. Urban ecological systems: Linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annual Review of Ecology and Systematics 32:127-157.

Pilgrim, E. M., S. A. Jackson, S. Swenson, I. Turcsanyi, E. Friedman, L. Weigt, and M. J. Bagley. 2011. Incorporation of DNA barcoding into a large-scale biomonitoring program: Opportunities and pitfalls. Journal of the North American Benthological Society 30:217-231.

Plaistow, S., and M. T. Siva-Jothy. 1999. The ontogenetic switch between odonate life history stages: Effects on fitness when time and food are limited. Animal Behaviour 58:659-667.

Poff, N. L. 1997. Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16:391-409.

Poff, N. L., J. D. Olden, N. K. M. Vieira, D. S. Finn, M. P. Simmons, and B. C. Kondratieff. 2006. Functional trait niches of North American lotic insects: Traits-based ecological applications in light of phylogenetic relationships. Journal of the North American Benthological Society 25:730-755.

Polhemus, J. T. 2008. Aquatic and semiaquatic Hemiptera. Pages 385-423 in R. W. Merritt, K. W. Cummins, and M. B. Berg (editors). An introduction to the aquatic insects of North America. 4th edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, B. Statzner, and I. R. Wais De Badgen. 1988. Biotic and abiotic controls in river and stream communities. Journal of the North American Benthological Society 7:456-479.

Purcell, A. H., C. Friedrich, and V. H. Resh. 2002. An assessment of a small urban stream restoration project in northern California. Restoration Ecology 10:685-694.

Rankin, M. A., and J. C. A. Burchsted. 1992. The cost of migration in insects. Annual Review of Entomology 37:533-559.

Reich, P., and B. J. Downes. 2003a. Experimental evidence for physical cues involved in oviposition site selection of lotic hydrobiosid caddis flies. Oecologia (Berlin) 136:465-475.

Reich, P., and B. J. Downes. 2003b. The distribution of aquatic invertebrate egg masses in relation to physical characteristics of oviposition sites at two Victorian upland streams. Freshwater Biology 48:1497-1513.

Reich, P., and B. J. Downes. 2004. Relating larval distributions to patterns of oviposition: Evidence from lotic hydrobiosid caddisflies. Freshwater Biology 49:1423-1436.

Resh, V.H., R.H. Norris, and M.T. Barbour. 1995. Design and implementation of rapid assessment approaches for water resource monitoring using benthic macroinvertebrates. Australian Journal of Ecology 20:108-121.

Resh, V. H., L. A. Bêche, and E. P. McElravy. 2005. How common are rare taxa in long-term benthic macroinvertebrate surveys? Journal of the North American Benthological Society 24:976-989.

Richardson, J. S., and R. J. Danehy. 2007. A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. Forest Science 53:131-147.

Ricketts, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. American Naturalist 158:87-99.

Ricklefs, R. E. 1987. Community diversity: Relative roles of local and regional processes. Science 235:167-171.

Rosenberg, D. M., and V. H. Resh. 1993. Freshwater biomonitoring and benthic macroinvertebrates. Chapman and Hall, New York.

Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. Science 241:1460-1466.

Roughgarden, J. 1989. The structure and assembly of communities. Pages 203-226 *in* J. Roughgarden, R. M. May, and L. A. Levin (editors). Perspectives In Ecological Theory. Princeton U.P., Princeton, New Jersey.

Roy, A. H., A. D. Rosemond, M. J. Paul, D. S. Leigh, and J. B. Wallace. 2003. Stream macroinvertebrate response to catchment urbanisation (Georgia, U.S.A). Freshwater Biology 48:329-346.

Roy, A. H., A. L. Dybas, K.M. Fritz, and H. R. Lubbers. 2009. Urbanization affects the extent and hydrologic permanence of headwater streams in a midwestern US metropolitan area. Journal of the North American Benthological Society 28:911-928.

Rundle, S. D., D. T. Bilton, J. C. Abbott, and A. Foggo. 2007. Range size in North American *Enallagma* damselflies correlates with wing size. Freshwater Biology 52:471-477.

Sabo, J. L., and M. E. Power. 2002. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. Ecology 83:3023-3036.

Sanderson, R. A., M. D. Eyre, and S. P. Rushton. 2005. The influence of stream invertebrate composition at neighboring sites on local assemblage composition. Freshwater Biology 50:221–231.

Sato, M., Y. Kohmatsu, M. Yuma, and Y. Tsubaki. 2008. Population genetic differentiation in three sympatric damselfly species in a highly fragmented urban landscape (Zygoptera: Coenagrionidae). Odonatologica 37:131-144.

Savolainen, E., A. Saura, and J. Hantula. 1993. Mode of swarming in relation to reproductive isolation in mayflies. Evolution 47:1796-1804.

Smith, B. J., and K. J. Collier. 2000. Interactions of adult stoneflies (Plecoptera) with riparian zones II. Diet. Aquatic Insects 22:285-296.

Smith, B. J., and K. J. Collier. 2005. Tolerances to diurnally varying temperature for three species of adult aquatic insects from New Zealand. Environmental Entomology 34:748-754.

Smith, B. J., K. J. Collier, and N. J. Halliday. 2002. Composition and flight periodicity of adult caddisflies in New Zealand hill-country catchments of contrasting land use. New Zealand Journal of Marine and Freshwater Research 36:863-878.

Smith, R. F. 2006. Effect of urbanization on stream insect communities in adjacent headwater and downstream reaches. MS Thesis, University of Maryland, College Park, Maryland.

Smith, R. F., and W. O. Lamp. 2008. Comparison of insect communities between adjacent headwater and mainstem streams in urban and rural watersheds. Journal of the North American Benthological Society 27:161-175.

Smith, S., L. Gutierrez, and A. Gagnon. 2009. Maryland Streams - Take a Closer Look (4th ed.). Watershed Restoration Division, Maryland Department of Natural Resources. Annapolis, MD.

Sode, A., and P. Wiberg-Larsen. 1993. Dispersal of adult Trichoptera at a Danish forest brook. Freshwater Biology 30:439-446.

Spänhoff, B. 2005. Seasonal decline of body mass in adults of the wood-dwelling caddisfly *Lype phaeopa* (Psychomyiidae). Archiv Für Hydrobiologie 163:369-382.

Spänhoff, B., and J. Arle. 2007. Setting attainable goals of stream habitat restoration from a macroinvertebrate view. Restoration Ecology 15:317-320.

Stacey, P.B., V.A. Johnson, and M.L. Taper. 1997. Migration within metapopulations: The impact upon local population dynamics, p. 267-291, *In* I. Hanski and M. E. Gilpin (editors). Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego.

Statzner, B., N. Bonada, and S. Dolédec. 2008. Predicting the abundance of European stream macroinvertebrates using biological attributes. Oecologia 156:65-73.

Stevens, D. J., M. H. Hansell, J. A. Freel, and P. Monaghan. 1999. Developmental trade-offs in caddis flies: Increased investment in larval defense alters adult resource allocation. Proceedings of the Royal Society of London Series B: Biological Sciences 266:1049-1054.

Stocks, I. C. 2010. Comparative and functional morphology of wing coupling structures in Trichoptera: Annulipalpia. Journal of Morphology 271:152-168.

Stoeckel, J. A., D. W. Schneider, L. A. Soeken, K. D. Blodgett, and R. E. Sparks. 1997. Larval dynamics of a riverine metapopulation: Implications for zebra mussel recruitment, dispersal, and control in a large-river system. Journal of the North American Benthological Society 16:586-601.

Stranko, S., D. Boward, J. Kilian, A. Becker, M. Ashton, A. Schenk, R. Gauza, A. Roseberry-Lincoln, and P. Kazyak. 2007. Maryland Biological Stream Survey, Round Three Field Sampling Manual. Maryland Department of Natural Resources Publication # 12-2162007-190. Annapolis, MD

Strayer, D. L. 2006. Challenges for freshwater invertebrate conservation. Journal of the North American Benthological Society 25:271-287.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology and Evolution 19:46-53.

Sweeney, B. W. 1993. Effects of streamside vegetation on macroinvertebrate communities of White Clay Creek in eastern North America. Proceedings of the Academy of Natural Sciences of Philadelphia 144:291-340.

Sweeney, B. W., and R. L. Vannote. 1987. Geographic parthenogenesis in the stream mayfly *Eurylophella funeralis* in eastern North America. Holarctic Ecology 10:52-59.

Tokeshi, M., and K. Reinhardt. 1996. Reproductive behavior in *Chironomus anthracinus* (Diptera: Chironomidae), with consideration of the evolution of swarming. Journal of Zoology 240:103-112.

Travis, J. M. J., D. J. Murrell, C. Dytham. 1999. The evolution of density-dependent dispersal. Proceedings of the Royal Society of London B - Biological Sciences 266:1837-1842.

Urban, M. C., D. K. Skelly, D. Burchsted, W. Price, and S. Lowry. 2006. Stream communities across a rural-urban landscape gradient. Diversity and Distributions 12:337-350.

Utz, R. M., R. H. Hilderbrand, and D. H. Boward. 2009. Identifying regional differences in threshold responses of aquatic invertebrates to land cover gradients. Ecological Indicators 9:556-567.

Verberk, W. C. E. P., H. Siepel, and H. Esselink. 2008. Life-history strategies in freshwater macroinvertebrates. Freshwater Biology 53:1722-1738.

Vinson, M. R. and C. P. Hawkins. 1998. Biodiversity of stream insects: Variation at local, basin, and regional scales. Annual Review of Entomology 43:271-293.

Vogel S. 1981. Life in Moving Fluids: The Physical Biology of Flow. Princeton University Press, Princeton, NJ.

Wagner, R. 2005a. Spatial, temporal and competition effects on size and weight of caddisflies (Insecta, Trichoptera) in emergence traps. Archiv Fur Hydrobiologie 162:383-398.

Wagner, R. 2005b. The influence of stream water temperature on size and weight of caddisflies (Insecta, Trichoptera) along the Breitenbach 1983-1991. Archiv Für Hydrobiologie 163:65-79.

Wallace, J. B., and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology 41:115-139.

Walsh, C. J., A. K. Sharpe, P. F. Breen, and J. A. Sonneman. 2001. Effects of urbanization on streams of the Melbourne region, Victoria, Australia. I. Benthic macroinvertebrate communities. Freshwater Biology 46:535-551.

Walsh, C. J., A. H. Roy, J.W. Feminella, P. D. Cottingham, P. M. Groffman, and R. P. Morgan. 2005. The urban stream syndrome: Current knowledge and the search for a cure. Journal of the North American Benthological Society 24:706-723.

Waters, T. F. 1972. The drift of stream insects. Annual Review of Entomology 17:253-272.

Watts, P. C., J. R. Rouquette, I. J. Saccheri, S. J. Kemp, and D.J. Thompson. 2004. Molecular and ecological evidence for small-scale isolation by distance in an endangered damselfly, *Coenagrion mercuriale*. Molecular Ecology 13:2931-2945.

Werneke, U., and P. Zwick. 1992. Mortality of the terrestrial adult and aquatic nymphal life stages of *Baetis vernus* and *Baetis rhodani* in the Breitenbach, Germany (Insecta: Ephemeroptera). Freshwater Biology 28:249-255.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393-425.

White, D. S., and R. E. Roughly. 2008. Aquatic Coleoptera. Pages 571-671 in R. W. Merritt, K. W. Cummins, and M. B. Berg (editors). An introduction to the aquatic insects of North America. 4th edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Wiggins, G.B. 2004. Caddisflies: The Underwater Architects. University of Toronto Press, Toronto, Ontario, Canada.

Wilbur, H. M. 1980. Complex life cycles. Annual Review of Ecology and Systematics 11:67-93.

Wilcock, H. R., A. G. Hildrew, and R. A. Nichols. 2001. Genetic differentiation of a European caddisfly: Past and present gene flow among fragmented larval habitats. Molecular Ecology 10:1821-1834.

Wilcock, H. R., R. A. Nichols, and A. G. Hildrew. 2003. Genetic population structure and neighborhood population size estimates of the caddisfly *Plectrocnemia conspersa*. Freshwater Biology 48:1813-1824.

Wilcock, H. R., M. W. Bruford, R. A. Nichols, and A. G. Hildrew. 2007. Landscape, habitat characteristics and the genetic population structure of two caddisflies. Freshwater Biology 52:1907-1929.

Williams, J. C., C. S. ReVelle, and S. A. Levin. 2005. Spatial attributes and reserve design models: A review. Environmental Modeling and Assessment 10:163-181.

Winterbourn, M. J. 2005. Dispersal, feeding and parasitism of adult stoneflies (Plecoptera) at a New Zealand forest stream. Aquatic Insects 27:155-166.

Winterbourn, M. J., and A. L. M. Crowe. 2001. Flight activity of insects along a mountain stream: Is directional flight adaptive? Freshwater Biology 46:1479-1489.

Winterbourn, M. J., W. L. Chadderton, S. A. Entrekin, J. L. Tank, and J. S. Harding. 2007. Distribution and dispersal of adult stream insects in a heterogeneous montane environment. Archiv für Hydrobiologie 168:127-135.

Wooton, R. J. 2002. Design, function and evolution in the wings of holometabolous insects. Zoologica Scripta 31:31-40.

Wright, S. 1938. Size of population and breeding structure in relation to evolution. Science 87:430-431.

Young, T. P., D. A. Petersen, and J. J. Clary. 2005. The ecology of restoration: Historical links, emerging issues and unexplored realms. Ecology Letters 8:662-673.

Yuan, F. and M. E. Bauer. 2007. Comparison of impervious surface area and normalized difference vegetation index as indicators of surface urban heat island effects in Landsat imagery. Remote Sensing of Environment 106:375-386.

Yuan, L. L. 2010. Estimating the effects of excess nutrients on stream invertebrates from observational data. Ecological Applications 20:110-125.

Zhao, J., Z. Ouyang, W. Xu, H. Zheng, and X. Meng. 2010. Sampling adequacy estimation for plant species composition by accumulation curves – A case study of urban vegetation in Beijing, China. Landscape and Urban Planning 95:113-121.